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CONTENTS

Spiral systems in the vascular plants ..... *John H. Schaffner* 507

Structure and growth of the shoot apex in Ginkgo Biloba ..... *Adrianne S. Foster* 531

Some new and interesting late tertiary plants from Sucker Creek, Idaho-Oregon boundary ..... *Helen V. Smith* 557

New species of cacti from Guatemala, Mexico and Texas ..... *Elzada U. Clover* 565

Notes on American melastomes, including nine new species ..... *H. A. Gleason* 571

Index to American Botanical Literature 581

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Spiral Systems in the Vascular Plants[1]

JOHN H. SCHAFFNER

(WITH PLATES 22 TO 24)

The sporophytes of vascular plants usually develop a radially symmetrical stem or axis from a meristematic mass of dividing cells. This radial symmetry depends on a fundamental potentiality possessed by the interacting cell group. The bud, with or without an apical cell, not only develops the stem cylinder but in practically all living species also produces lateral appendages, or leaves, in the axils of which axillary buds may or may not be present. The fundamental, radially symmetrical system is also present in the sporphytes of all Bryophyta, altho they do not develop lateral appendages, except the expanded hypophyses of some mosses which may be regarded as continuous lateral appendages whose growth is also controlled by the inherent radial potentiality of the developing system. In the majority of Bryophyta the gametophyte has also evolved the radial potentiality and its superficial lateral appendages, or scales, are also developed in radially symmetrical spiral systems. The fundamental radial symmetry of the sporophyte may be modified so that the stem develops as an oval, quadrangular, triangular, or even decidedly flattened system, but such forms are secondary developments and the plant still shows the primary cylinder at various stages of its growth. When the sporophyte stem develops leaves they are so determined in their positions that after growth is completed, they form a spiral system of greater or less complexity and of greater or less mathematical regularity.

The spiral system is not only a characteristic of the leaf arrangement, or phyllotaxy, but involves also the structure of the vascular system and other tissues in the stem. The spiral structure is prominently in evidence in the skeletons of old stems of the tree prickly-pear, *Opuntia imbricata* (Haw.) Engelm., in which the specific spiral system can be determined as readily from the large gaps in the vascular cylinder as from the external leaf positions. The branches of *Cercis* and *Pedilanthus* and of many other plants show a zig-zag character in harmony with their alternate two-ranked leaf arrangement. The correspondence between the structural organization of the twig and leaf arrangement is clearly indicated by the five-angled pith and the five ridges on the bark of cottonwood twigs, *Populus balsamifera* L. The same relation is also prominently shown in young shoots of various species of blackberries, as in *Rubus frondosus* Bigel., by the five-angled pith and the five very prominent ridges on the

[1] Papers from the Department of Botany, The Ohio State University, No. 403.

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stem. Thus, it is evident that the leaf positions and the structural relations of the stem are primarily determined by the same fundamental potentiality. There is a fundamental potentiality of spiralization which determines the relative positions of the leaf incepts and the correlative interactions of these centers of growth activity in relation to each other and also determines the general arrangement of the tissue systems throuout the total mass of cells of the growing bud. The addition of a further potentiality to the hereditary complex which causes the production of internodes does not change the general spiral system but is to be regarded as only a third advance in the progressive complexity of the sporophyte stem along with the fundamental radial symmetry and potentiality for spiralization.

What the ultimate nature of this potentiality of spiralization may be cannot be surmised at present, but it is, nevertheless, something quite as definite as the force of crystallization in the various chemical substances. It is some internal correlative or coordinating interaction force or potentiality which determines the physiological gradients of the bud and the structural positions of the new incepts for leaves or other lateral organs as the growth of the bud proceeds. One thing is certain; the positions in the spiral systems are not primarily dependent on any predetermination of the structural elements of the stem already laid down, since the system may change in any given bud from one type to another. The differentiation of the structural elements is determined by physiological or physico-chemical forces in action at the time of growth. Thus, very profound reaction changes are especially in evidence when a bud changes from an alternate, two-ranked, vegetative system to a reproductive, trimerous or pentamerous system in the flower. Whatever the factors involved may be, the final result is produced by a combination of all the growth forces and growth processes active in the given system.

By controlling the ecological-physiological conditions, the writer was able in the hemp plant, *Cannabis sativa* L., to cause a change from opposite to alternate leaf arrangement at any level of stem development beyond the few opposite nodes which had already been determined in the plumule of the embryo. After rejuvenation of old plants the alternate leaf arrangement also frequently changes back again to the opposite condition (Schaffner, 1926). The change from one vegetative spiral system to a succession of others during the ontogenetic growth gradient is easily seen in many common plants.

Recently it has become the vogue to attempt to explain all growth reactions on the basis of hormones and growth-promoting substances, but such agents can only be secondary in the determination of spiral systems. The accumulation of hormones may stimulate cell division at certain

points but the real problem is to discover the mechanism which determines the mathematical positions where the substances accumulate, if there is such a relation between growth and the supposed stimulating substance.

There is at present much superficial reasoning about the influence of cosmic rays, violet rays, temperature, etc. as primary causal agents of evolution, but a study of the spiral systems as well as of numerous other biological systems in relation to the general taxonomic system shows that all such reasoning is beside the mark. There is no evident correspondence between the presence of the supposed causal agents and the systems themselves. For example, the grasses, numbering over 4,000 species, with numerous tribes, subtribes, and genera, have been on the earth for an enormous period of geological time and at present extend from the Equator to the Arctic regions, from the water to the desert, from sea level to the vegetation limit of high mountains, yet they all have the alternate, two-ranked spiral system in their vegetative shoots. The sedges are close lower relatives of the grasses and are nearly as widely distributed over the earth, often growing in the same habitats and thus subjected for ages to the same physical agents—heat and cold, violet rays, cosmic rays, etc.—as the grasses, but this has not given them the same spiral system. The vast majority of them have the spiral three-ranked leaf arrangement, frequently with three-angled stems. A few species have their leaves arranged in complex multispirals.

By various authors, as in Schwendener's mechanical hypothesis, the stimulus determining the positions of the incipient leaf members was assumed to be the pressure exerted by the developing leaves covering the growing bud. But such an explanation represents a purely superficial view, since many stems with only minute, vestigial leaves have very definite spiral systems, as in many cacti and spurges.

When one studies various phylogenetic series, it soon becomes evident that in the lower levels of the series there is frequently much variation in the number of spirals produced even on the same stem and between branches of the same plant, and that the control of the spiral development goes thru certain evolutionary sequences, which at the higher levels commonly end in one of a few determinate, stable systems, unless some unusual hereditary factor is introduced, such as a special expansion potentiality active either in the vegetative or reproductive phase or in both. These culminating systems become practically fixed and unchangeable in entire families or even larger groups and are of great importance in determining taxonomic relationships.

Apparently the lower vascular plants had comparatively simple spiral systems, as is the case in the living species, and these became more com-

plex in various lines thru the progressive evolution of larger buds with no corresponding increase in the efficiency of the internal correlative control or coordinating interactions from the centers of activity to the surrounding cells. Thus, the larger the bud the greater the number of spirals produced at any given level, and thus sometimes an enormous difference on stems, branches, or flowers of different sizes, as is prominently shown in nearly all species of *Equisetum*. With the evolutionary advancement in the efficiency of the correlative control from the determined centers, the vegetative spiral system will be simplified again on the higher evolutionary levels even tho there be a decided increase in the size of the growing bud. Two prominent culmination types become established in many phyletic lines of Pteridophyta, Gymnospermae, Monocotylae, and Dicotylae. The two normal culminations or determinate types are (1), the alternate, two-ranked arrangement, in which the center of activity has the largest controlling influence possible in a radially symmetrical system, taking in the entire cross-section at the given growth level; and (2), the opposite, four-ranked system which becomes the normal, determinate limit when the pitch of the clockwise and counter-clockwise primary spirals becomes the same, with the centers of activity at each node reduced to the smallest symmetrical number, namely two. Unusual or abnormal, extreme systems are the opposite two-ranked arrangement and the unispiral system. Both of these are very rare. An advanced system may be evolved in the plant which may be expressed only at a certain stage of the ontogeny. Thus, in *Cyperus* the extreme, two-ranked condition appears only in the branches of the inflorescence. In some species of *Helianthus* the opposite, four-ranked system is developed in the juvenile stage while in the later periods of growth the five-ranked arrangement is expressed. The same is true for the hemp, *Cannabis sativa* L. Thus it must be recognized that a more recently acquired spiral reaction system may come to expression either in the early juvenile stage or in the later growth stages of the ontogeny.

It is an interesting fact that the growth of true roots rarely if ever shows an indication of a definite spiral control. The root branches seem to develop in a rather haphazard fashion. The potentiality for spiralization seems to be completely latent, altho as soon as a stem bud develops on a root it immediately begins a spiral activity, shown by the spiral arrangement of its lateral organs. In *Stigmaria* fossils, which represent branched stems penetrating the ground like root systems from the base of the tree trunk, the root-like structures have the positions of leaves in spirals and probably have some relation to leaf structures.

Elaborate systems of phyllotaxy have been developed, but these have dealt especially with abstract mathematical and philosophical theories on

the one hand or on the other with fantastic teleological speculations as to the causal relations of the different spiral systems to their environments or to supposed special advantages of one type or another of leaf arrangement to the individual. There was little of practical value in these speculations, and Sachs was inclined to dismiss the subject from serious consideration as "playing with figures." But these rhythmical processes of growth are a very prominent part of the phenomena of life and as such demand study from various points of view. The abstruse and complicated mathematical treatments and speculations could not arouse very much enthusiasm in the non-mathematical botanists, who both in the past and at present constitute nearly the entire taxonomic clan.

The general system of phyllotaxy still in vogue lays especial stress on the angle of divergence, or the proportion of the distance around the stem that one leaf is removed from the one next in age, as in the Fabonacci series but the sequence of the order of appearance may be considerably changed thru various causes and thus cannot be used, except in the simplest systems, as a basis for fundamental mathematical speculations. The ontogenetic gradients may be modified by determinate factors, by zygomorphic or inequilateral factors or by expansion factors at various points of development. In the more primitive type of typical flowers, as in *Lilium* for example, the members appear in acropetal succession. In advanced types the cycles are often practically synchronous in origin. In some, the incepts of the carpels may appear before those of the stamens, or the incepts of the sepals may develop after those of the stamens. In *Capsella* the petals are the last to appear. In zygomorphic flowers there is often a decided difference in the appearance of the incepts of the members of a single cycle. But these changes in sequence of the ontogenetic development do not change the fundamental nature of the spiral systems involved, and one cannot tell from the matured structures in what sequence the different members originated. From a practical point of view, we are more especially interested in the character of the completed systems and should deal with them as such. Nor are we concerned whether the systems are mathematically exact. They can at best be only approximate. The exact mathematics of any material system is only in the mind of the mathematician. Flattened stems, as in some species of *Opuntia*, may still show an evident spiral system. Dorsiventral shoots are due to secondary potentialities which are imposed on the more primitive radial systems and the typical cylindrical spirals are thus modified, but such cases do not at all invalidate the spiralization as a fundamental system.

The subject of phyllotaxy also developed a difficult terminology with such terms as divergence angle, orthostiches, parastiches, decussate, genet-

ic spiral, genetic cycle and Fabonacci ratios. The "cycle" is defined as the portion of the genetic spiral between any two leaves directly above one another, a meaning quite different from that in general use when a flower is said to be cyclic, tricyclic, pentacyclic, etc.

The so-called Fabonacci series of fractions, named from its discoverer, is as follows: 1/2, 1/3, 2/5, 3/8, 5/13, 8/21, 13/34, 21/55, etc. It corresponds to a selected list of ratios that can be found in the spiral systems of plants, but, as will appear below, the system as a whole is very much more complex. This Fabonacci series of fractions was in the past even compared with a somewhat similar series of approximate numbers representing the relative distances of the planets from the sun, usually known as "Bode's law."

The teleological explanations given in the past for the various systems of phyllotaxy are, as would be expected, commonly extremely absurd and inconsistent. The Fabonacci relation being the commonest, it was assumed to be possibly the most primitive type. Another especially fantastic notion has been held that the present spiral systems of the vascular plants are the outcome of a long series of progressive adaptations. Bonnet assumed that the spiral arrangements gave the optimum advantage for transpiration, while Wiesner gave an equally fantastic teleological explanation, that the Fabonacci relation gives the optimum angle for maximum exposure to light in photosynthesis. Such teleological explanations are easily laid to rest when one has advanced far enough in taxonomic studies to learn that similar spiral systems are present where the leaves are vestigial or are reduced to minute scales, as in many cacti, milkweeds, spurges, etc., and as in the scale leaves on the ordinary branches of *Pinus*, the bracts on the cup of the fruit in *Quercus*, and the scales on the surface of the pericarp of the fruit of some palms as in *Raphia* and *Calamus*. As well might one seek to find a teleological explanation for the angles of the various species of crystals of chemical compounds.

A SIMPLE METHOD FOR REPRESENTING SPIRAL SYSTEMS

After many years of taxonomic study and teaching of advanced students, the writer has attempted to develop a simple, definite, and practical method for constructing projection diagrams of all types of spiral systems, whether simple or complex, and also to devise a system of numerical formulae that would indicate the complete and exact nature of the various types and their ordinary modifications. The aim was especially to develop a system that could be used conveniently for both vegetative shoots and flowers. In the present paper the intention is to present the simple facts of the spiral systems so that the more important patterns can be used con-

veniently in systematics and in the discovery of evolutionary trends, sequences, and limits in the various phyletic lines.

All normal types of mature spiral systems, developed on a cylinder, contain four main morphological characteristics: (1) one or more clockwise primary spirals, (2) one or more counter-clockwise primary spirals, (3) two or more ranks, or radii, either straight or spiral, and (4) one or more secondary spirals whenever the clockwise and counter-clockwise primary spirals are unequal in number; or if the primary clockwise and counter-clockwise spirals are equal in number there are no secondary spirals but the leaves or other members are in cycles. Explanations of these terms are given below. Since the various spiral systems all have these four characteristics, they can all be represented by a formula of four numbers with dashes between them. The clockwise primary spirals are always written first; the second number represents the counter-clockwise primary spirals; the third number represents the ranks or radii; and the fourth number represents the secondary spirals or indicates that the system is cyclic. The direction of the spirals is always to be determined in the direction of growth, namely from the bottom of the shoot to the top.

METHOD FOR CONSTRUCTING PROJECTION SPIRAL DIAGRAMS

The procedure for making a projection diagram of a spiral system is as follows: Take, for example, a comparatively simple spiral system as represented in a twig of *Populus balsamifera* L. (Cottonwood), a young shoot of *Rubus frondosus* Bigel., a long potato tuber of the "Idaho Baker" type of *Solanum tuberosum* L., a carpellate cone of *Pseudotsuga taxifolia* (Lam.) Britt., or a twig of an oak. These all have either two or three clockwise primary spirals and two or three counter-clockwise primary spirals. The *Populus* or the *Rubus* will show a prominent 5-angled pith and five ridges on the surface of the stem corresponding to the five vertical ranks of leaves. The numerical formula will thus be 2-3-5-1 or 3-2-5-1. The spiral system that has the clockwise primary spirals smaller in number than the counter-clockwise primary spirals is said to be a right-handed system and one that has the clockwise primary spirals larger in number than the counter-clockwise primary spirals is said to be a left-handed system. Since the vertical ranks curve in the same direction as the smaller number of primary spirals, the "right-handedness" or "left-handedness" of the system can also be determined by observing the spiral direction of the ranks whenever the curvature in these shows distinctly. Clockwise spiral ranks indicate a right-handed system, counter-clockwise spiral ranks indicate a left-handed system. The curvature, or degree of pitch, of the spiral in the ranks usually depends on the size of the ratio of difference

between the clockwise and counter-clockwise primary spirals, unless there is a distinct torsion of the entire system. The ranks, or radii, are always equal to the sum of the clockwise and counter-clockwise primary spirals with one characteristic exception. The secondary spirals are equal to the difference between the clockwise and counter-clockwise primary spirals and will curve in the same direction as the larger number of primary spirals. If the primary spirals are equal in number the difference will, of course, be zero, which indicates, as intimated above, that there are no secondary spirals but that the secondary system, with one exception, is cyclic.

In determining the primary spirals, always take the next higher, often partly overlapping leaf or other organ beyond the first by moving radially and vertically from the first to the second. Care must be taken, especially if internodes are present, that the primary spiral is not confused with a secondary. With a little practice the primary spirals can be determined without difficulty, especially if one uses a string or marks the successive units as the spiral is traced out.

To construct the projection diagram of the given right-handed system, with the formula 2-3-5-1, one proceeds as follows (fig. 1):

Draw a series of circles, suitably spaced, with pencil so that these guiding lines may be erased, if desired, after the diagram is completed. In figure 1 they have been drawn in ink for distinct reproduction. In a complex multispiral system the circles must be close together in order that a sufficient sample of the system may be shown. Next, draw the required number of radii, properly spaced, and correct these to indicate the spiral pitch of the ranks. These need not be measured accurately for ordinary purposes, since the essential nature of the system will be evident from the primary spirals to be drawn. The radii may be numbered with Roman numerals, always in a clockwise direction for the sake of simplicity and uniformity and always beginning with the uppermost one, as shown in figures 1, 10, 14, 15, 16, and 20.

Now to locate the positions of the members making up the spiral system, taking figure 1 as a model, begin with the upper radius, numbered I, and place a dot on the intersection with the first circle on the outside. Beginning with this point, count the circles or intersections on the radius, —1, 2, 3, 4, 5, 1,—placing a dot on the last "1" and so proceed until the available circles have been counted. To locate the positions on the second radius, pass from the top position on the first radius along the outermost circle, in a clockwise direction, to the second radius (II), and count the number of the clockwise spirals on this, namely,—1, 2, 1,—and place a dot on the second 1; then as before, beginning with this position, count the

intersections toward the center,—1, 2, 3, 4, 5, 1,—marking the second "1" and so proceed until the available intersections have been counted. From any dot on this second radius pass to the third radius (III) and as before count,—1, 2, 1,—again marking the second "1." From this position then one can count the fives either toward the center or the circumference until the proper positions are all marked. One proceeds thus until the proper positions are all marked on all the radii. In case one wishes to proceed in a counter-clockwise direction from the starting point one must count the number of the counter-clockwise primary spirals to get the first position on the radius (V), namely—1, 2, 3, 1,—as will be evident by an inspection of figure 1.

After all the positions have been marked, the clockwise and counter-clockwise primary spirals may be drawn thru them. It is best to draw the spirals first with a pencil and then trace them in ink. In order to have a uniform system of graphs, the writer always represents the clockwise primary spirals with continuous lines, the counter-clockwise primary spirals with broken lines, the radii with lines of small dots, and the secondary spirals, not shown in figure 1, with lines of large dots. The clockwise primary spirals may be numbered with Arabic numerals and the counter-clockwise primary spirals with Arabic numerals in parentheses as in figures 1, 10, 16, and 21. Right-handed spiral systems are represented by figures 1, 2, 3, 4, 6, 7, and 15, and left-handed systems by figures 5, 8, and 20. Apparently all spiral systems may develop, by the law of chance, as right-handed or left-handed systems on branches of the same or of different plants.

Projection diagrams of spiral systems may, of course, be constructed without drawing guiding circles by simply drawing the proper radii and measuring off the given positions with a ruler, but this method is more apt to lead to mistakes in determining the proper positions.

SECONDARY SPIRALS AND CYCLES

A study of the spiral systems clearly indicates that no single "genetic spiral" can be used conveniently to analyze the numerous spiral systems developed in the vascular plants, since the secondary spirals can be one up to a large number. After the primary system has been constructed, secondary spirals are often clearly in evidence and they are sometimes easily seen on the plant itself (see figs. 3, 4, 6, 7, and 8, in which the secondaries are represented). The secondary spirals are determined by skipping one rank or radius when passing from one position to the next and as stated above they curve in the direction of the larger number of primary spirals, when proceeding from the circumference to the center,

or in the direction of the smaller number of primaries if one begins in the center. When the numbers of the primary spirals are large and the number of the secondary spirals is small, as one, two, or three, much counting can be saved in constructing the projection diagrams by determining the positions for the secondary spirals after the fundamental positions have been located on a single radius. If there is but one secondary spiral, as in figures 6 and 8, there will be but one-interval difference from one position to the next on the third radius as one proceeds, if there are two secondaries, as in figure 7, there will be a two-interval difference on the third radius, etc. If the system is cyclic the fact will be indicated by the fourth number of the spiral formula being a zero and the ranks will be parallel to the axis of the shoot unless there is a general torsion of the whole system. In the culmination type of the alternate two-ranked system, 1-1-2-0, there is an apparent exception to the rule that a zero in the fourth number indicates a cyclic system, but since such a system has come to unity, the zero may be interpreted as a cycle with but one member which has attained the highest efficiency of the correlative interaction, controlling the entire cross-section of the bud at the given level (fig. 16).

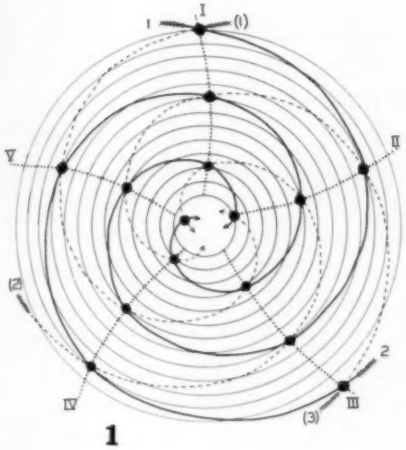
All types of cyclic systems can be represented by the same construction method as is used for the spiral systems with secondary spirals, but a simpler method is available, since by placing the positions alternately at the intersections of successive circles and radii, a similar projection diagram will be obtained. This method has long been used in representing the cyclic-spiral systems as represented by the common cyclic flowers of the Angiospermae. It may also be advantageously used for the diagrams of the cones of *Equisetum* and for some of the individual cones of *Zamia*, etc. When one considers the problem as a whole, it becomes evident that the cyclic systems are only special cases of the fundamental spiral system. Typical cyclic systems are represented by figures 11, 13, 19, and 21.

EXAMPLES OF REPRESENTATIVE SPIRAL SYSTEMS

In general, as stated above, the more primitive members of a phylogenetic series have variable spiral systems while advanced groups often have very stable systems, especially if they have attained one of the

Explanation of Plate 22

Fig. 1. Twig of *Populus balsamifera* L., spiral system 2-3-5-1.
Fig. 2. Branch of *Lycopodium obscurum* L., 3-4-7-1.
Fig. 3. Carpellate cone of *Zamia integrifolia* Ait., 6-7-13-1.
Fig. 4. Carpellate cone of *Pinus caribaea* Mor., 5-8-13-3.
Fig. 5. Carpellate cone of *Zamia integrifolia* Ait., 6-5-11-1.
Fig. 6. Staminate cone of *Araucaria angustifolia* (Bert.) O. Ktz., 10-11-21-1.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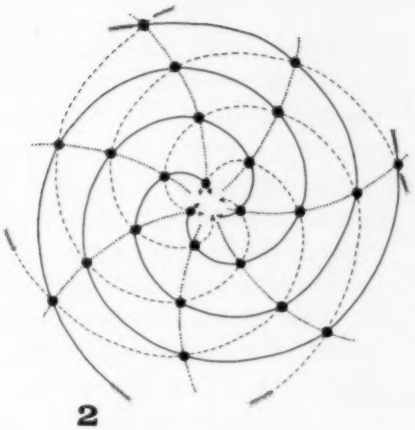
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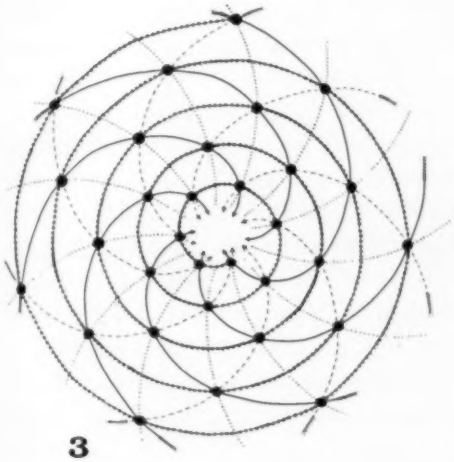
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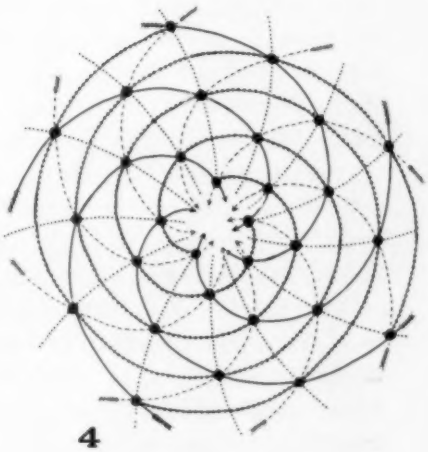
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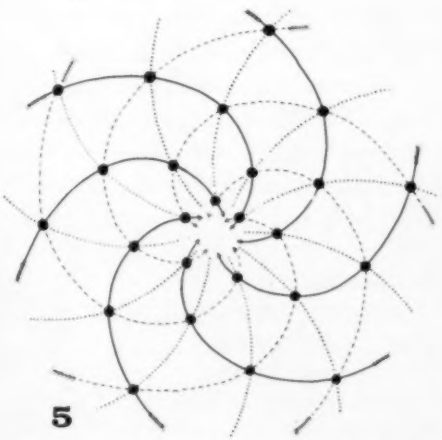
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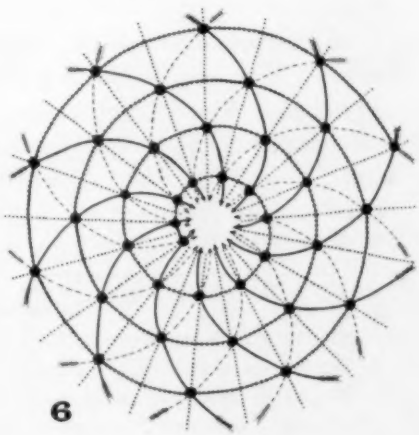
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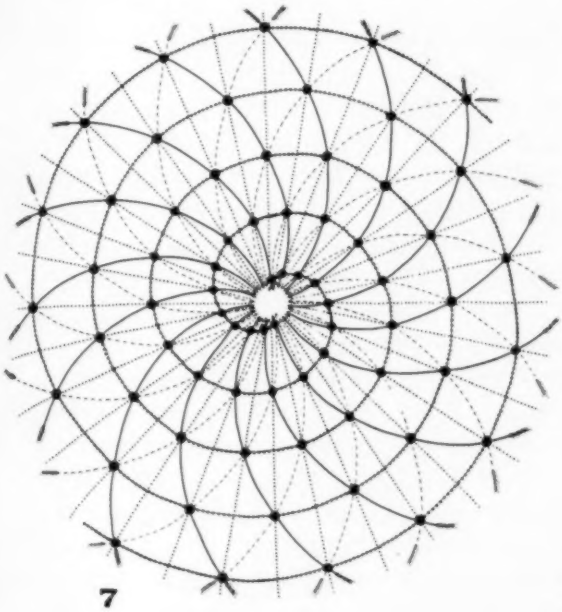
several determinate culmination types of spiralization. If, however, an expansion hereditary factor has been added to the cell without a corresponding increase in the potentiality determining the control of an area around the incipient center from which a leaf is developed, then the spirals may again be decidedly increased and again show marked variability. *Lycopodium lucidulum* Mx. is one of the more primitive flowerless types of the living Lepidophyta. Its spiral system is commonly 4-5-9-1 or 5-4-9-1, or 4-4-8-0. Very often all three types are on different branches of the same plant. In the following examples only the formulae for right-handed systems are usually given, but it is to be understood that the corresponding left-handed sytems of any given type are just as common either on the same plant or on different individuals. *Lycopodium annotinum* L. has the leaves in 4-5-9-1, 4-4-8-0, and 3-4-7-1 spiral systems and the same types for the sporophylls in the cones. In *Selaginella arenicola* Und. leaf spirals were noted of the formulae 4-4-8-0 and 3-4-7-1, and there are probably others present, while in the cones the sporophylls are reduced to the opposite 4-ranked arrangement, a 2-2-4-0 spiral system. In the numerous higher species of *Selaginella* both leaves and sporophylls are quite constantly of the opposite four-ranked type. In *Equisetum*, the lower species are exceedingly variable both in the leaf and sporophyll whorls, the number in a cycle varying with the size of the bud. In the most reduced species, *E. scirpoides* Mx., all cones and aerial stems constantly have trimerous whorls. The branches of *E. pratense* Ehrh. also, have trimerous whorls quite regularly. In one of the extreme water-ferns, *Azolla caroliniana* Willd., the leaf arrangement has attained one of the determinate limits, the alternate two-ranked condition, or 1-1-2-0 spiral system.

In various more advanced lines of vascular plants, the primary bud becomes very large without a corresponding increase in the evolution of the correlative interaction control and in consequence, as intimated above, the complexity of the spiral systems is greatly increased, as in species of *Cycas*, *Palmaceae*, *Yucca*, *Fourcroya*, *Cactaceae*, etc. A few stems of *Cycas revoluta* L. available for study had developed spiral systems as follows: 15-20-35-5, 18-21-39-3, 20-28-48-8, 21-34-55-13, and 34-21-55-13. A stami-

Explanation of Plate 23

Fig. 7. Staminate cone of *Dioon edule* Lindl. (1936), spiral system, 15-17-32-2.
Fig. 8. Staminate cone of *Dioon edule* Lindl. (1937), 18-17-31-1.
Fig. 9. Branch of *Opuntia imbricata* (Haw.) Engelm., 4-6-10-2.
Fig. 10. Dorsiventral branch of *Lycopodium obscurum* L., 3-3-6-0.
Fig. 11. Staminate cone of *Zamia integrifolia* Ait., 7-7-14-0.
Fig. 12. Flattened twig of *Libocedrus decurrens* Torr., 2-2-4-0



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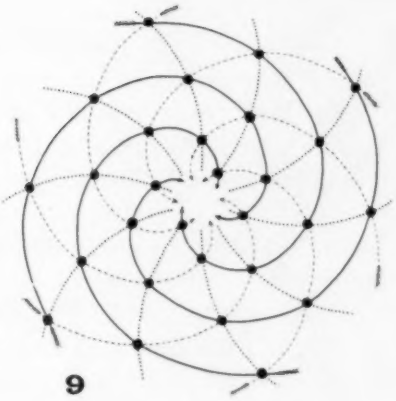

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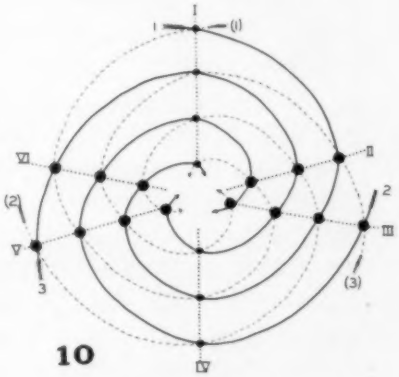

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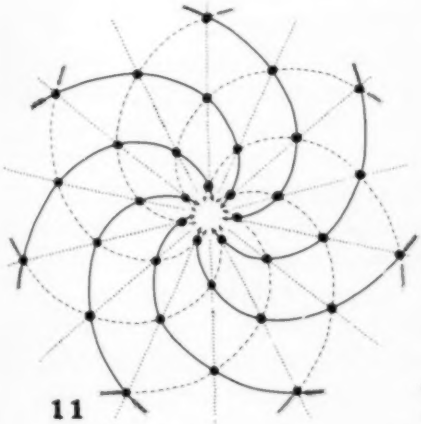

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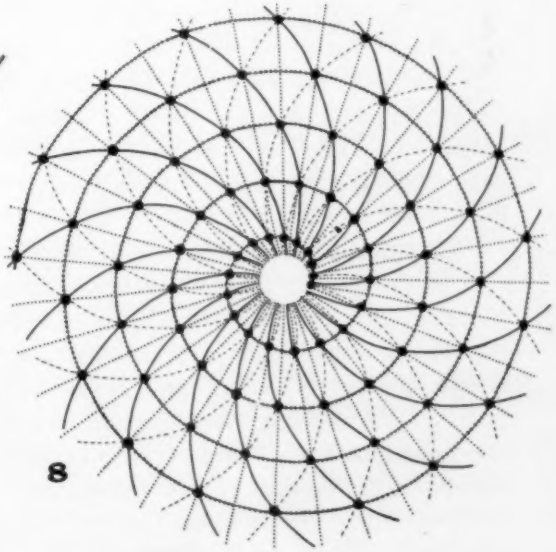

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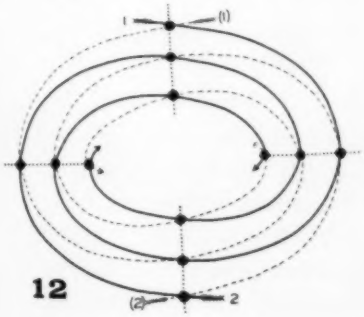

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nate cone of the same species had the stamens arranged in a 14-17-31-3 spiral system. The staminate cones of *Dioon edule* Lind. usually vary on the same plant from one blooming season to the next. A staminate plant in the greenhouse had a cone in 1936 with the formula 15-17-32-2 (fig. 7), and in 1937 a cone with the formula 18-17-35-1 (fig. 8). A single carpellate cone available for study gave the formula 8-13-21-5 which corresponds to the Fabonacci fraction 8/21. The new formula shows that the system is right-handed with five secondary spirals while the old Fabonacci fraction does not give this information directly. The flowers of *Zamia integrifolia* Ait. (*Z. floridana* DC.) are exceedingly variable and make a very good object for studying spiral systems. The following types of carpellate cones were found: 3-3-6-0, 4-4-8-0, 4-5-9-1, 5-5-10-0, 5-6-11-1, 6-5-11-1, 6-6-12-0, 6-7-13-1. Staminate cones studied gave the following formulae: 4-3-7-1, 5-5-10-0, 6-6-12-0, 6-7-13-1, 7-7-14-0. There are no doubt other types. Any complicated spiral system may for convenience be called a multispiral. A few carpellate cones of *Zamia furfuracea* Ait. were available for study. These had the following spiral systems: 3-5-8-2, 5-3-8-2, 4-4-8-0, 4-5-9-1, 6-5-11-1. A number of staminate cones of *Araucaria angustifolia* (Bert). Ktz. showed the following spiral formulae: 10-9-19-1, 10-10-20-0, 11-9-20-2, 10-11-21-1, 11-11-22-0, 11-12-23-1, 12-10-22-2, 12-11-23-1, and 12-12-24-0. The carpellate cones of many pines have the 5-8-13-3 spiral system, among which may be mentioned *Pinus caribaea* Mor., *P. taeda* L., *P. torreyana* Carr., *P. sabiniana* Dougl., *P. coulteri* D. Don., *P. nigra* Arnold, *P. virginiana* Mill., and *P. glabra* Walt. *Picea abies* (L.) Karst. also has carpellate cones with the 5-8-13-3 formula. Staminate cones of *Pinus nigra* Arnold vary considerably. Study of only a few cones gave the following spiral systems: 7-6-13-1, 7-7-14-0, 8-8-16-0, and 9-8-17-1. *Tsuga canadensis* (L.) Carr. usually has carpellate cones with a 2-3-5-1 or a 3-2-5-1 spiral arrangement but in a small collection one was found with a 4-3-7-1 system.

The alternate two-ranked spiral system, 1-1-2-0, is present in vegetative shoots of great numbers of the Angiospermae. This system, since it is a culmination reaction type, often shows a remarkable constancy, as in the four thousand species of grasses, most of the 10,000 to 15,000 species of Orchidaceae, the thousand species of the Iris family, most of the Scitaminales and numerous other Monocotylae. Large numbers of families and genera of Dicotylae have also attained this extreme, as for example *Asimina*, *Pedilanthus*, *Tilia*, *Cercis*, *Hamamelis*, *Ulmus*, *Celtis*, *Fagus*, *Planera*, *Ostrya*, *Betula*, etc. The opposite four-ranked system, 2-2-4-0, is also evolved in many families and genera. Occasionally this system may pass over in individual branches to a trimerous, cyclic condition, and

perhaps some trimerous genera and species are mutations from this type. Among the families with all or most of the species with opposite four-ranked leaves may be mentioned, Selaginellaceae, Juniperaceae, Gnetaceae, Oleaceae, Asclepiadaceae, Gentianaceae, Verbenaceae, Lamiaceae, Aceraceae, Aesculaceae, Hypericaceae, Dipsacaceae, Valerianaceae, Caprifoliaceae, and Caryophyllaceae. An abnormal system, apparently derived from the opposite four-ranked condition, is the opposite two-ranked spiral system, 2-2-2-0, in which the normal relation between the primary spirals and the number of ranks or radii does not hold. Two genera which have this extreme system are *Chamaesyce* and *Tribulus* (fig 18). It is interesting to note that in both genera the axillary buds or branches have a definite alternate two-ranked arrangement, only one of each pair of leaf axils producing a functional bud, which is alternate with the bud at the next node. Thus, we have here, in the same plant, both an alternate and an opposite position reaction. Another advanced type, but apparently not a culmination, is the spiral three-ranked condition, 1-2-3-1 spiral system, which is so prominently developed in the screw-palms, or Pandanaceae (fig. 15). This type is also very evident in the common greenhouse umbrella-plant, *Cyperus alternifolius* L., whose leaves, on a long reproductive scape, form three prominent clockwise or counter-clockwise spiral ranks. A common dicotyl genus with this leaf arrangement is *Alnus*.

In *Pandanus* the writer observed a bud sport in which the three-spiral changed suddenly to a straight, alternate two-ranked leaf arrangement and grew thus for five years, when it fell back just as suddenly to the normal, spiral three-ranked condition again (Schaffner 1919 and 1925). In this connection it is interesting to note that the two higher families of the Pandanales, Sparganicceae and Typhaceae, have two-ranked leaves. The spiral ranks of *Pandanus* and the umbrella-plant are apparently not caused by a twisting of the tissues of the stem axis, but the torsion is due to the fact that of the two sets of primary spirals one is twice the number of the other. In *Rhoeo* and *Musa* the torsion of the two ranks apparently is due to a forward movement in the successive leaf positions produced by some factor influencing the interaction control system.

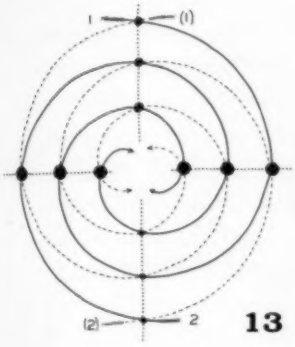
The most extreme and at the same time most puzzling spiral system is the unispiral, either clockwise, 1-0-0-0, or counter-clockwise, 0-1-0-0. Here the system is reduced to the ultimate limit of simplicity and altho the organization of the bud is apparently still radially symmetrical the reaction which produces the positions of the leaves is asymmetrical. A genus in which this type is present is *Costus*, as in *C. speciosus* (Koenig) Sm., belonging to the Zingiberaceae. This family normally has the alternate two-ranked spiral system. This unispiral of *Costus* has given rise to much

discussion and difference of opinion as to its cause. Apparently the condition is dependent on a definite hereditary factor for an inequilateral reaction in the growing bud. In the two highest families of the Scitaminales, Marantaceae and Cannaceae, the flowers, altho structurally radially symmetrical, are inequilateral in the development of their parts. A peculiar unispiral sometimes develops in the shoots of various species of Equisetum. Instead of the normal cyclic sheaths a spiral sheath may suddenly develop and usually after a time disappear just as suddenly, the shoot going back to the normal condition. Sometimes the ridges of one or more internodes above the spiral zone show a spiral twist or torsion (Schaffner 1927). In these cases there is apparently no addition of a new hereditary factor but simply a new reaction of the original heredity complex in the cells.

In the hypogynous Liliaceae, the lowest of the subclass Liliiflorae, one finds the *Aloe* group which contains a whole series of stages in the evolution of the spiral system from very complex multispirals to the normal determinate limit, the alternate two-ranked leaf arrangement. However, the early juvenile stage usually shows a very simple spiral system, even down to the alternate two-ranked condition, and only later is a more complex type developed. This is, of course, commonly the case in many groups, since it takes some considerable period of growth to develop the large-sized buds from which the multispirals develop. The writer has not had the opportunity to study any of the large tree species with complex spiral systems but among the species with complex multispirals are *Aloe rubrolutea* Schinz., *A. speciosa* Bak., and *A. aethiopica* (Schweinf.) Berg. The following species have been studied: *Haworthia reinwardtii* Haw., spiral formula 3-5-8-2; *Aloe arborescens* Mill., 2-3-5-1; *Kniphofia uvaria* (L.) Hook., 2-2-4-0; *Aloe variegata* L. and *A. viscosa* (L.) Haw., 1-2-3-1; *A. plicatilis* (L.) Mill., *A. haemanthifolia* Mar. and Berg., and *A. cooperi* Bak., 1-1-2-0; *A. ciliaris* Haw., 1-1-2T-0. The symbol T indicates a torsion system and that the ranks are definitely spiral where one would usually expect straight ranks.

Explanation of Plate 24

Fig. 13. Dorsiventral branch of *Lycopodium complanatum* L., spiral system, 2-2-4-0.
Fig. 14. Dorsiventral branch of *Selaginella kraussiana* A. Br., 2-2-4-0.
Fig. 15. Inflorescence shoot of *Cyperus alternifolius* L., 1-2-3-1.
Fig. 16. Twig of *Ulmus americana* L., 1-1-2-0.
Fig. 17. Stem of *Rhoeo discolor* Hance, 1-1-2T-0.
Fig. 18. Stem of *Chamaesyce preslii* (Guss.) Arth., 2-2-2-0.
Fig. 19. Branch of *Lycopodium lucidulum* Mx., 4-4-8-0.
Fig. 20. Sweet corn ear (6-rowed) of *Zea mays* L., 2-1-3-1.
Fig. 21. Dent corn ear (24-rowed) of *Zea mays* L., 6-6-12-0.



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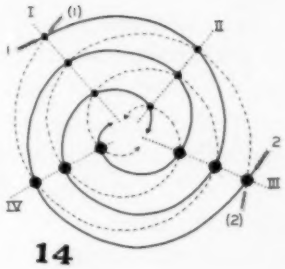

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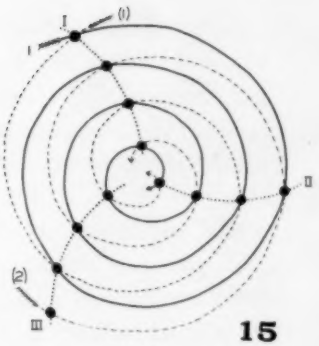

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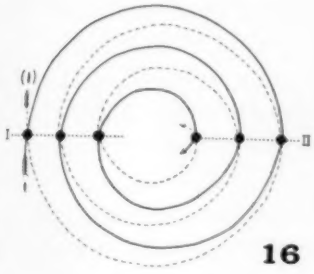

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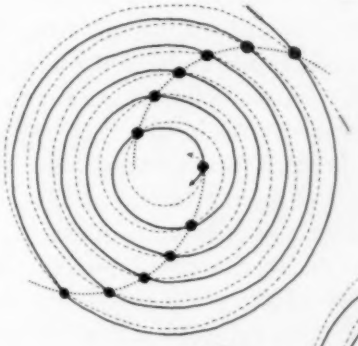

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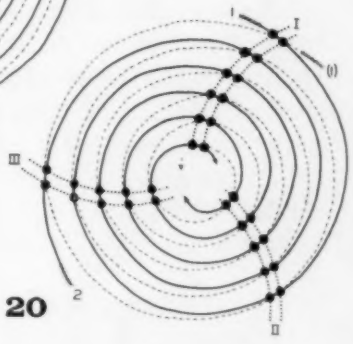

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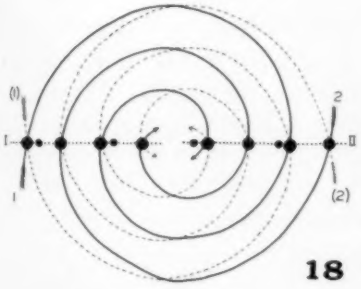

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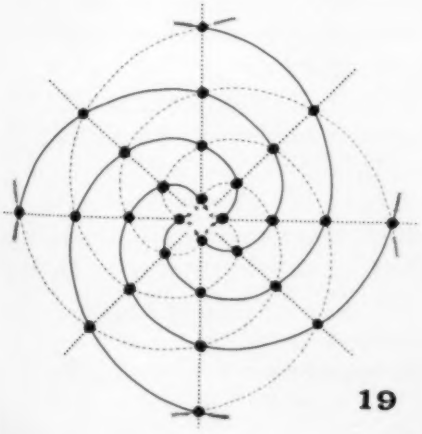

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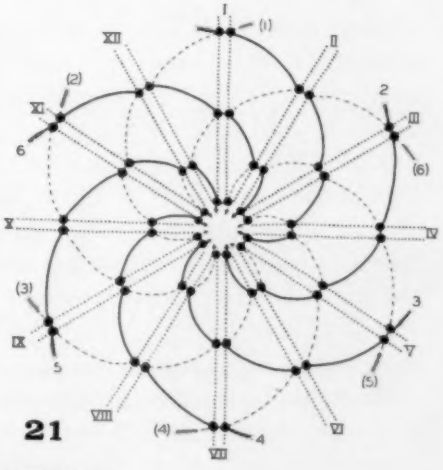

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Variations in the spiral arrangement of the leaves is shown by the twigs of *Morus alba* L. The main axis, water shoots or vigorous branches may have a 2-3-5-1 arrangement or a 1-2-3-1 system and the more slender lateral twigs normally have the alternate two-ranked arrangement, 1-1-2-0. This condition apparently indicates that the white mulberry has attained the final potentiality of the two-ranked system but in such a weak condition that it is only expressed in the smaller, least vigorous buds. Similar conditions are frequently met in other groups. Thus in the oaks, *Quercus*, the leaves have the common five-ranked arrangement, 2-3-5-1, while in the chestnut, *Castanea dentata* (Marsh.) Borkh., the small lateral branches usually have the alternate two-ranked leaf arrangement while the more vigorous main branches have the 2-3-5-1 system. In the related beech, *Fagus americana* Sweet, the most advanced and specialized of the three genera, the branches usually have only the alternate two-ranked leaf arrangement. The juvenile arrangements do not, however, necessarily indicate the more primitive condition.

A plant which shows very prominently the relation between the primary spiral system and the vertical ranks is the common greenhouse species, *Euphorbia lacta* Haw. Very frequently one can observe among its various, thick, fleshy branches some with three spiral ridges, 1-2-3-1, some with four ridges, 2-2-4-0, and some with five ridges, 2-3-5-1. The primary spirals can easily be determined by twining strings around the stems thru the leaf positions or clusters of spines. The three-ranked joints usually show a decided, spiral twist.

EFFECT OF THE EVOLUTION OF SPECIAL EXPANSION FACTORS

Altho there is a general evolutionary movement in most advanced phylogenetic series toward a reduction and simplification of the spiral system, yet hereditary expansion factors are frequently introduced which may enlarge either the vegetative or reproductive buds and axes very decidedly and may thus cause a great increase in the number of spirals produced in the expanded part. With the introduction of such a factor, the hereditary reaction may again bring out decided fluctuations in the number of spirals produced. This condition is usually prominent in the disk of the common cultivated sunflower, *Helianthus annuus* L., and in the ear of Indian corn, *Zea mays* L. The great increase in the number of spirals in some stems of cacti has apparently also been caused by the evolution of expansion factors along with fleshiness.

The development of a great disk as in the common sunflower brings in a new mathematical problem, since there is a constant increase of the number of spirals on the disk from the center to the margin. In such a case

one can count the clockwise and counter-clockwise primary spirals at the outer part of the disk and simply write these two numbers in the formula. A disk $4\frac{1}{2}$ inches in diameter had 55–86 primary spiral formula; one 11 inches in diameter had 83-122; one 15 inches in diameter had 144-89. It is evident that with a further enlargement of the disk, the number of the spirals could be much greater.

In the Andropogoneae, the spikelets are usually in pairs and thus if one wishes to ascertain the spiral arrangement in an ear of Indian corn, *Zea mays* L., a pair of grains must be taken for each position. The simplest ear has two double rows of grains and is thus a 1-1-2-0 spiral system. From this rare condition one can find, among the varieties, a continuous series up to the 6-6-12-0 (24-rowed) type and far beyond. The 6-rowed ear, 1-2-3-1 spiral system, is also exceedingly rare (fig. 20). A diagram of a 24-rowed ear is shown in fig. 21. A 14-rowed ear has a 3-4-7-1 or 4-3-7-1 spiral system. The ear often changes from a higher to a lower system at or near the middle. Thus an ear was found having 16 rows in the lower half and 12 in the upper half; another one had 20 rows in the lower half and 18 in the upper half. When the change is abrupt, as it was in these two cases, there is irregularity on the transition zone but the normal double-row, spiral system is soon established again with the reduced numbers.

EXAMPLES FOR A SYSTEMATIC STUDY OF THE SIMPLER SPIRAL SYSTEMS

In the list below only right-handed formulae are given. All those with unequal numbers of clockwise and counter-clockwise primaries will also occur in the left-handed condition.

I. Examples of complex multispiral systems are represented by Figs. 6, 7, and 8.

II. Cyclic spiral system 7-7-14-0, a staminate cone of *Zamia integrifolia* Ait. (fig. 11).

III. Spiral system 6-7-13-1, a carpellate cone of *Zamia integrifolia* Ait. (fig. 3).

IV. Spiral system 5-8-13-3, involucre of artichoke, *Cynara scolymus* L., inflorescence fruit of the pineapple, *Ananas comosus* (L.) Merrill, carpellate cone of *Pinus caribaea* Mor. (fig. 4).

V. Cyclic spiral system 6-6-12-0, a carpellate cone of *Zamia integrifolia* Ait., vegetative shoots of *Galium triflorum* Mx. and *G. concinnum* T. & G.

VI. Spiral system 5-6-11-1, a carpellate cone of *Zamia integrifolia* Ait.

VII. Cyclic spiral system 5-5-10-0, a staminate cone of *Zamia integrifolia* Ait., a large stem of *Selaginella arenicola* Und. This is a pentamerous ten-ranked system.

VIII. Spiral system 4-6-10-2, a branch of *Opuntia imbricata* (Haw.) Engelm. (fig. 9).

IX. Spiral system 4-5-9-1, branches of *Lycopodium lucidulum* Mx. and *L. annotinum* L. and main stem of *L. obscurum* L.

X. Cyclic spiral system 4-4-8-0, some branches of *Lycopodium lucidulum* Mx., some cones of *L. obscurum* L., some branches of *Equisetum arvense* L., some stems of *Selaginella arenicola* Und., stem of *Galium circaezans* Mx. This is a tetramerous, eight-ranked system (fig. 19).

XI. Spiral system 3-5-8-2, carpellate cones of *Pinus strobus* L. and *Sequoia washingtoniana* (Winsl.) Sudw., branch of *Opuntia imbricata* (Haw.) Engelm.

XII. Spiral system 3-4-7-1, some shoots of *Selaginella arenicola* Und., some cones of *Lycopodium obscurum* L., some branches of *Opuntia imbricata* (Haw.) Engelm. (fig. 2).

XIII. Cyclic spiral system 3-3-6-0, *Equisetum scirpoides* Mx., *Salvinia natans* (L.) Hoffm., *Juniperus communis* L., some branches of *Catalpa speciosa* Ward., flowers of *Yucca*, *Lilium*, *Iris*, etc. This is a ternate six-ranked system (fig. 10).

XIV. Spiral system 2-3-5-1, twigs of *Rhus glabra* L., young shoots of *Asparagus officinalis* L., *Quercus* sp., *Populus* sp. This is the five-ranked spiral system and is very common (fig. 1).

XV. Cyclic spiral system 2-2-4-0, the higher species of *Selaginella*, *Thuja*, *Gnetum*, *Naias*, *Acer*, *Salvia*, *Bidens*, etc. This is the opposite, or dimerous, four-ranked system and is a very common culmination type (figs. 13, 14).

XVI. Spiral system 1-2-3-1, *Pandanus* sp., *Alnus* sp., reproductive shoot of *Cyperus alternifolius* L. This is the alternate spiral three-ranked system (fig. 15).

XVII. Cyclic spiral system 2-2-2-0 with the axillary buds and branches in the 1-1-2-0 spiral system, *Chamaesyce* sp., *Tribulus terrestris* L. This is the rare, abnormal, opposite two-ranked system (fig. 18).

XVIII. Alternate two-ranked torsion system with the two ranks prominently spiral, 1-1-2(T)-0, *Cordyline terminalis* Kunth, *Rhoeo discolor* Hance, *Musa sapientum* L. (fig. 17).

XIX. Spiral system 1-1-2-0, *Azolla*, *Graminaceae*, *Iridaceae*, *Asimina*, *Tilia*, *Cercis*, *Ulmus*, *Zygocactus truncatus* (Haw.) K. Schum. This is the normal alternate two-ranked arrangement with straight or nearly straight ranks and is the normal culmination type of the spiral system in many plant groups (fig. 16).

XX. Unispiral system, 1-0-0-0 or 0-1-0-0, *Costus speciosus* (Koenig) Sm. and shoots or zones of shoots of *Equisetum* sp. This is a very rare abnormal type, showing an inhibition of the fundamental, radially symmetrical reaction system.

SUMMARY STATEMENT OF RELATIONS IN THE SPIRAL SYSTEMS AND METHODS OF CONSTRUCTING FORMULAE AND PROJECTION DIAGRAMS

1. All normal spiral systems, developed on a cylinder, have both clockwise and counter-clockwise primary spirals, the direction to be determined in the direction of growth. In constructing projection diagrams of spiral systems the base is always to be represented at the outer part of the circle and the upper part in the center.

2. If the number of clockwise primary spirals is smaller than the number of counter-clockwise primaries, the system is said to be right-handed and if the number of clockwise primary spirals is larger than the number of counter-clockwise primaries, the system is said to be left-handed.

3. The number of vertical ranks, or radii, is equal to the sum of the clockwise and counter-clockwise primary spirals, except in the rare, opposite two-ranked arrangement which is an abnormal type.

4. The vertical ranks, or radii, curve in the same direction as the smaller number of primary spirals. A right- or left-handed system can then also frequently be determined by the spiral direction of its vertical ranks. If the ranks curve in a clockwise direction the system is right-handed, if counter-clockwise, the system is left-handed.

5. The secondary spirals are equal in number to the difference between the clockwise and counter-clockwise primary spirals and are determined

by skipping one radius in going from one position to the next on the projection diagram or on the spiral cylinder.

6. The secondary spirals curve in the same direction as the larger number of primary spirals in the system.

7. If the clockwise and counter-clockwise primary spirals are equal in number, there are no secondary spirals but the parts are in cycles and the ranks, or radii, are straight and parallel to the axis unless there is torsion of the entire system. The cyclic condition is produced whenever the pitch of the clockwise and counter-clockwise spiral screws becomes equal. In the extreme, alternate two-ranked system, the rule that the zero indicates a cyclic system does not hold unless it is assumed that the one member controlling the entire cross-section of the growing bud at the given level makes a cycle.

8. Any spiral system can be conveniently represented by a formula of four numbers as, for example, the common, right-handed, five-ranked type by 2-3-5-1, or the opposite four-ranked type by 2-2-4-0. The first number represents the clockwise primary spirals, the second number the counter-clockwise primary spirals, the third number the ranks, or radii, and the fourth number the secondary spirals, or if the number is zero a cyclic system without any secondary spirals.

9. The two possible, normal evolutionary culmination types are the opposite four-ranked and the alternate two-ranked systems, both of which are very abundant in the higher evolutionary levels of certain phyletic lines.

10. The two abnormal culmination types, which form exceptions to the general rules of spiralization are the opposite two-ranked and the unispiral conditions, in both of which there is some exceptional factor which changes the normally, radially symmetrical reaction of the growing stem bud.

11. Any spiral type may be distorted by growth torsion or by twisting of the whole system.

12. Irregularities in positions may be developed in any system during growth when the reaction changes from one type to another thru the influence of internal or external environmental conditions, especially when the cell system contains factors for more than one type of reaction, as in those plants which have potentialities for both the primary-secondary spiral system and the primary spiral-cyclic system. Certain abnormal developments, as faciation for example, may cause very great disturbances, but these abnormalities have no direct bearing on the problem of the fundamental nature of the spiral systems.

HISTORICAL DEVELOPMENT AND BIBLIOGRAPHY OF SOME RECENT PAPERS

Consideration of the historical development of the theories of phyllotaxy may properly begin with Bonnet, who published a paper on the subject in 1754. Later, in the years 1830–1835, Schimper and Braun elaborated a system of phyllotaxy and their treatment became the common basis for both criticism and further theory. In the meantime, many investigators, both before and after Schimper and Braun, considered the subject, among whom may be mentioned Goethe, the brothers Bravais, Wiesner, Hofmeister, Schwendener, Eichler, C. de Candolle, and Warming.

Below is given a partial list of important references to the literature which has appeared since the beginning of the present century. However, there are many other papers of importance, besides the ones mentioned, which may be studied by those who are interested in the recent treatment of the subject and the theoretical views entertained.

OHIO STATE UNIVERSITY
COLLEGE OF AGRICULTURE
COLUMBUS, OHIO

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Structure and Growth of the Shoot Apex in Ginkgo Biloba

ADRIANCE S. FOSTER

(WITH 12 FIGURES AND PLATES 25 TO 27)

INTRODUCTION

Although an extensive literature has developed regarding the morphology and phylogenetic relationship of *Ginkgo*, cf. bibliography in Sprecher (1907), Seward and Gowan (1900), Chamberlain (1935), no careful investigation seems to have been made of the structure of the shoot apex of this primitive gymnosperm. In the meagre literature devoted to this aspect of *Ginkgo*, two opposed interpretations have appeared. Strasburger (1872 p. 327) concluded that the growing point is differentiated into three well-defined histogens, viz.: an independent "protoderm," a two-layered periblem and a central plerome. Fankhauser (1882, p. 4) confirmed this interpretation with the qualification that the limits between the periblem and plerome are not always distinct. In contrast, Solms Laubach (1884, p. 154, Plate XVIII, fig. 2) described and figured in surface view, a large apical cell with definite segments, in the shoot apex of the seedling. The observations of Sprecher (1907, p. 15), at least in respect to the embryo, failed to support either of these views. Sprecher found that periclinal divisions occur in the superficial layer (i.e. Strasburger's "protoderm") and that furthermore the periblem and plerome arise from a common group of initials. Unfortunately, Sprecher did not investigate the structure of the growing point of the buds of spur and long shoots of the tree.

The evident need for a thorough study of the organization and growth of the shoot apex of *Ginkgo* prompted the present study. In addition, it was hoped that information on this primitive gymnosperm might throw some light upon the disputed organization of the growing point in the Coniferales[1] and hence might lead to a better understanding of the evolution of the apical meristem in seed plants.

It is a pleasure to express my thanks to my wife for her invaluable assistance in the preparation of the illustrations used in this paper. I am also appreciative of the help given by Dr. Otto Schüepp of Basle with several difficult points of theory. Acknowledgement is made for the grant furnished by the Board of Research of the University of California.

MATERIALS AND METHODS

The material used in the present investigation was obtained from several large microsporangiate trees growing near and on the campus of

[1] For reviews of the literature cf. Koch (1891), Schüepp (1926), Korody (1937).

the University of California, Berkeley. During April, May and early June of 1937 terminal buds of vigorous spur shoots were collected two or three times a week. Additional bud material of both spur and long shoots was secured late in the dormant period as well as during the period of shoot elongation in 1938.

To facilitate the rapid penetration of the formalin-acetic acid-alcohol solution used as a killing and fixing reagent, the outer foliar organs were first removed from the buds and the shoot apices then gently evacuated in the killing fluid. The material was dehydrated, cleared in xylene and embedded in paraffin by the usual technique. Serial longitudinal and transverse sections were cut at a thickness of 6, 7 or 8 microns and stained with tannic acid and iron chloride in conjunction with safranin (cf. Foster, 1934). Since accurate orientation of the shoot apices on the block-carrier of the microtome is impossible, it was necessary to section numerous buds in order to secure a significant number of "median" series. The information presented in this paper is based upon a detailed study of nearly 100 longitudinal and about 50 transverse series.

The drawings in this article were prepared as follows: the sections chosen for illustrations were photographed using a high dry objective. Prints were then made on "mat" paper upon which the desired cell outlines and contents were lightly traced in pencil. The final step consisted in placing the prints in a solution which removed the photographic image, after which the penciled outlines were retraced in ink. Unless otherwise stated, all text figures represent a magnification of ×17.5 diameters. The photomicrographs with the exception of text figs. 1 and 2 were taken under oil immersion and have not been reduced for reproduction.

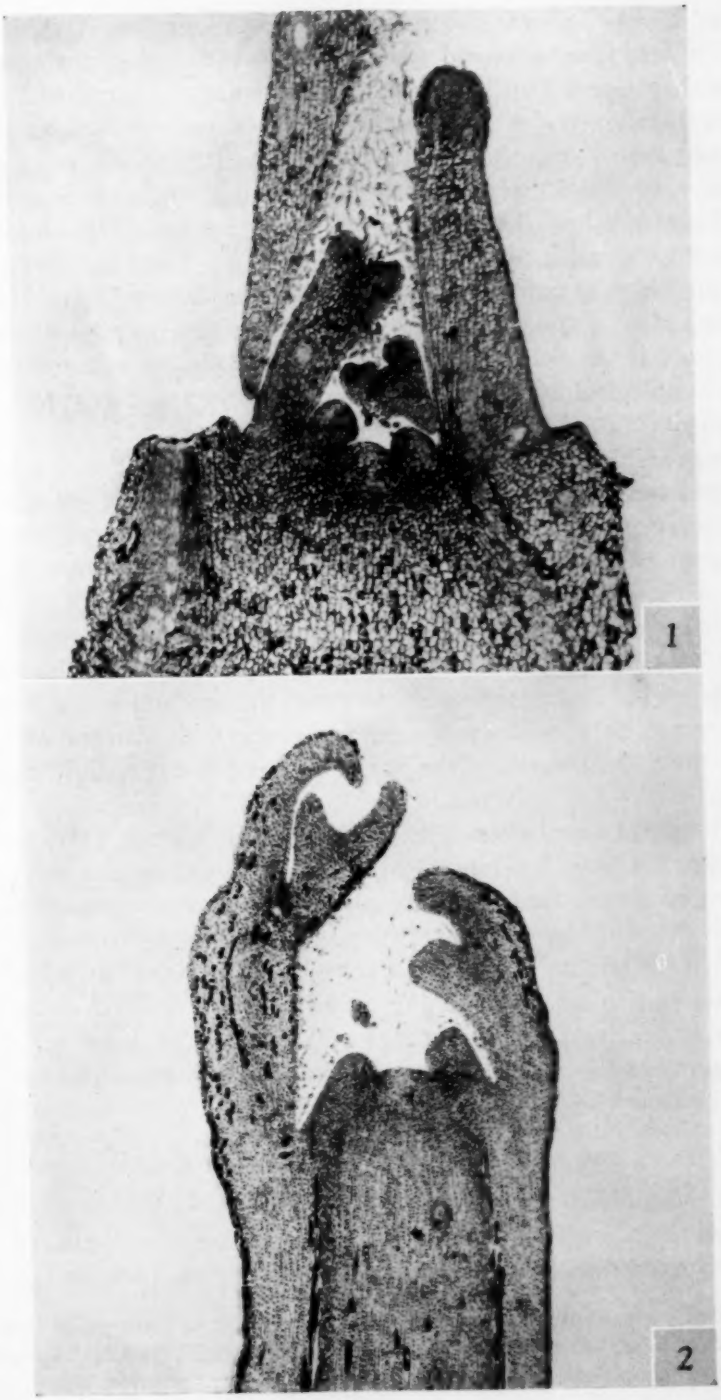
GENERAL MORPHOLOGY AND PERIODICITY OF THE SHOOT SYSTEM

Before describing the structure and growth of the shoot apex, it will be necessary to note briefly certain features of the morphology and periodic development of the vegetative shoot system. As is well known, two well-

Explanation of Figures 1–2

Fig. 1. Median longisection of the upper portion of a spur shoot, April 15, showing the meristematic apex between the two youngest bud-scale primorida. Note the zone of lightly-stained central mother cells, the absence of distinct internodes and the abrupt transition from the rib meristem to the broad expanding pith. ×35. (The detailed structure of the apex of this shoot is shown on Plate 25, fig. 1.)

Fig. 2. Longisection of the upper portion of a long shoot April 18, showing the meristematic apex between the two youngest foliage-leaf primordia. Contrast the prominence of the rib meristem in the future pith and cortical regions and the consequent formation of distinct internodes with the condition in the spur shoot in Fig. 1. Two secretory cavities are seen developing in the central region of the rib meristem. ×35. (The detailed structure of the apex of this shoot is shown on Plate 27, fig. 1.)



Figures 1–2

defined types of shoots occur in *Ginkgo*, viz.: long shoots, characterized by elongated internodes and relatively small pith and cortex and spur or dwarf shoots, with much abbreviated internodes and comparatively large pith and cortical regions. Observation shows however that these two types of shoots are not morphologically "fixed" in character since the terminal bud of a spur shoot may give rise to a long shoot, and conversely the apical bud of a long shoot may fail to form extended internodes, thereby producing a dwarf shoot (cf. Doak 1935 p. 46, fig. 24). Examination of the trees used in this study indicated that while the "lateral" spur shoots may exhibit a similar growth rhythm for many successive years, a "terminal" spur shoot is very often followed the next season by a true long shoot. The physiological aspects of the mutability and periodicity of spur and long shoots in *Ginkgo* clearly deserve investigation.

From an histogenetic standpoint, it is significant that no fundamental difference has been found in the cellular organization of the growing points in the two types of shoots. As is shown clearly in Figures 1 and 2, the differences seem to lie basically in the relative extent of and duration of activity in the rib meristem of cortex and pith regions. In the spur shoot, the vertical extent of the rib meristem is short and is followed abruptly by the region of expanding and maturing parenchyma; internodal elongation consequently is at a minimum. In contrast, the production of a long shoot is always associated with a prolonged period of cell division and cell elongation in the rib meristem and the inevitable formation of well-defined internodes.

As is true of many gymnosperms (Koch 1891, Korody 1937) shoot development in *Ginkgo* involves the annual formation of a series of cataphylls followed by the production of foliage leaves. However, unlike the situation in *Abies* described by Korody (1937 p. 29) there is little appreciable difference in the relative size or shape of the growing point in *Ginkgo* during the scale and foliage-leaf forming periods (figs. 1 and 2). Although no attempt has been made in this study to contrast the developmental history of cataphyll and foliage leaf, a brief description will be given later of the early phases in the initiation of these organs.

THE ZONAL STRUCTURE OF THE SHOOT APEX

The most distinctive feature of the meristem of the shoot apex[2] of *Ginkgo* is the segregation of its cells into a number of well-defined *zones*. Fig. 3 represents an effort to depict schematically the position and direc-

[2] Throughout the present paper, the entire apical region of a bud will be designated as the "shoot apex." The more restricted term "growing point" has such a vague and ambiguous connotation that its use will be avoided as far as possible.

tions of growth of the cells in each zone. Without doubt, Zone II is the most distinctive and unique structural region of the growing point. When viewed in median longisection, this zone appears as a prominent cup-shaped group of large, polygonal, lightly-stained cells which are situated in the upper median region of the shoot apex (cf. Plates 25 and 27). From a careful observation of many "median" series it is evident that *cell enlargement*, rather than cell division is the dominant process characteristic of Zone II. As a consequence, this zone always remains clearly demarcated from the remaining tissue of the growing point, which is composed of much smaller and more frequently dividing cells. The region of transition

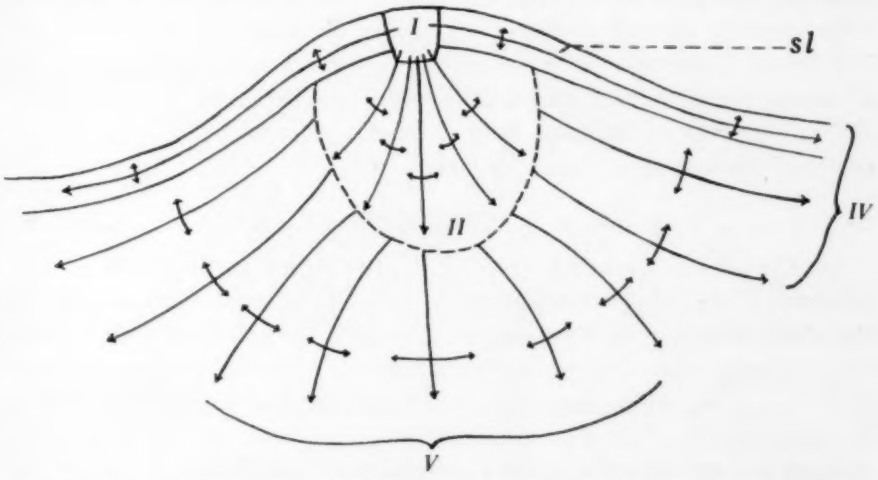


Fig. 3. Diagram illustrating the zones and their mode of growth in the shoot apex of *Ginkgo*. Zone I represents the position of the *apical initial group*, from which by anticlinal and periclinal divisions respectively the surface layer (sl) and the internal tissue of the growing point originate. Zone II is the prominent cup-shaped mass of large, slowly dividing *central mother cells*. As indicated by the arrows, volume growth predominates in this zone. The lateral and basal margins of the group of central mother cells (indicated by the broken U-shaped outline) constitute Zone III, characterized by the smaller size and frequency of division of its cells. From this "transition" zone arise the peripheral subsurface layers (Zone IV) and the rib meristem (Zone V). The long arrows in the surface layer and in Zones IV and V indicate the prevailing directions of growth in respect to the surface of the growing point. In the surface layer and in Zones II, IV, and V, the small double arrows represent the relative amount of growth at right angles to the prevailing direction.

from Zone II to Zones IV and V, as seen in longitudinal view, consists of a U-shaped zone of small, tabular cells; from the latter radiate the densely cytoplasmic inner peripheral layers (Zone IV) and the filamentous cell groups of the rib meristem (Zone V). In transverse sectional view, the

U-shaped "zone of transition" appears as a cylinder of cambial-like cells which entirely surround the cells of Zone II (Plate 26, figs. 1, 2). Since Zone II clearly functions as the common point of propagation of most of the internal tissue of the growing point, its component cells will be termed "central mother cells." Nevertheless, it must be emphasized that the *ultimate* source of all cells in the shoot apex of *Ginkgo* is represented by the *apical initial group* (Zone I, fig. 3; figs. 4, 5, 6c, 7a, 11, 12). These surface cells occupy the median apical region of the growing point and by means of anticlinal and periclinal divisions add new cells respectively to the surface layer (sl in all text figures) and to the central mother cells. However, as will be shown later, the behavior of the cells of the apical initial group seems entirely subordinated to the *growth of the shoot apex as a whole* and in no sense is comparable to the orderly and precise segmentation typical of certain vascular cryptogams. With this general account of the organization and growth of the shoot apex of *Ginkgo*, a more detailed description can be given now of the various zones.

APICAL INITIAL GROUP (*Zone I, fig. 3*)

At the outset, it may be stated that no evidence has been found of the existence of a single permanent apical cell. The presence of such a cell in the shoot apex of the seedling, as described by Solms-Laubach (1884) seems very questionable, particularly since his observations were confined to a surface view of the growing point. Furthermore Lyon (1904 p. 278) in his careful embryological study of *Ginkgo* emphasized that shoot and root growing points "arise through a localization of growth activity out of one general meristematic tissue; and hence from the first are many-celled meristems."

Because of the broad and only slightly elevated form of the growing point, perfect transverse sections of the surface were only rarely obtained in the present study. Figure 4 represents an approximately transverse section through the surface layer and shows a central group of four prominent cells which doubtless represent initials. It is obvious from this preparation, as well as from serial longisections, however, that no regular plan of segmentation exists. New anticlinal and periclinal division walls are inserted at varying angles and frequencies and only rarely is it possible to trace a whole series of surface or internal cells to the repeated division of any of the initials. In other words the geometrical apex of the shoot is occupied by a group of cells, variable in number, from which all the remaining tissue originates. Using Schüepp's (1926 p. 45) terminology, these initiating cells will be designated collectively as the "apical initial group." In their general mode of growth and variable sequence of cleavage, the

cells of the apical initial group in *Ginkgo* are fundamentally similar to the single tier of initials characteristic of *Abies*, *Picea* and *Pinus* (Korody 1937) and of various species of *Lycopodium* (Härtel 1938).

A comparison of serial longisections through many shoot apices in *Ginkgo* demonstrates that while anticlinal, periclinal and periclinal-oblique divisions occur in the apical initial group, there is no regular sequence in these planes of cleavage. According to the recent investigations of Härtel (1938), anticlinal divisions predominate over periclinal divisions in the apical initial group in the shoot apex of *Lycopodium*. Whether a similar condition occurs in *Ginkgo* is not apparent from the present study. It is conceivable however, that significant differences in respect to the relative

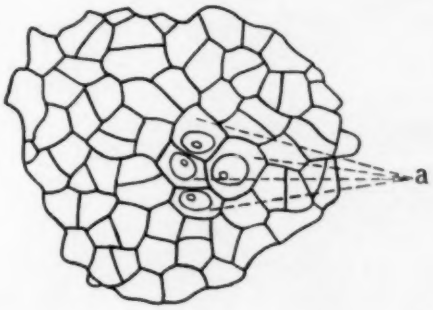


Fig. 4. Surface view of the apex of a spur shoot showing a central group of apical initials (a) and the irregular arrangement of the surface cells derived from them.

frequency of periclinal and anticlinal divisions might be detected in a statistical comparison of long and spur shoots. Some preparations of spur shoots indicate that anticlinal divisions have dominated for a time resulting in the propagation of a regular series of surface cells (figs. 8, 9, 10). Very frequently however, one or more cells in the apical initial group enlarge in an anticlinal direction and then divide by strictly periclinal or periclinal-oblique walls (figs. 5, 6a, 7a, 11, 12; Plate 25, fig. 2; Plate 27, fig. 2). The behavior of the daughter cells resulting from such divisions is highly variable. Often, each cell divides anticlinally resulting in a group of four cells, the outer two of which continue to function as initials while the inner two become incorporated in the zone of central mother cells (fig. 7a). In some instances, this "decussate" type of division may occur in several adjacent cells. Figure 11 for example reveals the products of a trio of unusually prominent apical initials, the laterals of which have divided in a decussate manner while the median cell pair is preparing for the anticlinal division. In other preparations however, the interpretation of the cell net in the apical initial group is complicated by (1) the irregular

sequence of anticlinal and periclinal divisions and (2) the wall-bending and enlargement of the inner segments (figs. 6b, 6c, 12). Similar difficulties have been encountered by Härtel (1938 p. 141, figs. 16–19) in the shoot apex of *Lycopodium*.

Lastly it must be noted that, as is true of many conifers (Koch 1891, Korody 1937) and *Lycopodium* (Härtel 1938), periclinal divisions are not confined to the apical initial group in *Ginkgo* but may occur at any point in the surface layer (figs. 6c, 6d, 7b, 10; Plate 25, figs. 1, 2; Plate

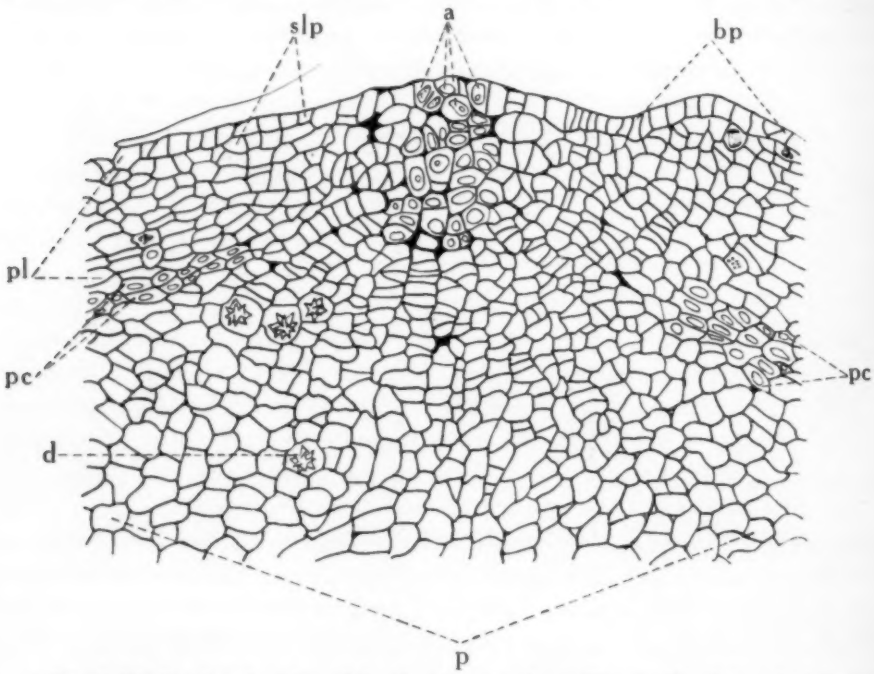


Fig. 5. Median longisection of the tip of a spur shoot, illustrating the typical segregation of the meristem into well-defined zones. ×161. In this and all following figures, the extent of the zone of central mother cells is represented by the large nucleated cells and localized "wall-thickenings" are shown by heavy black outlines.

Legend for all figures: *a*, cells of the apical initial group; *bp*, primordium of bud scale; *d*, druse; *p*, pith; *pc*, procambium, *pl*, zone of peripheral layers; *r*, zone of rib meristem; *slp*, periclinal division of surface layer.

27, figs. 1, 2). Consequently, as represented by the small double arrows in Figure 3, the surface layer cannot be regarded as a "dermatogen" (Hanstein 1868) or "protoderm" (Strasburger 1872, footnote p. 325) but on the contrary represents the point of origin of a variable portion of Zone IV. From a cytological standpoint, it is interesting to note that in contrast to the slightly larger and more lightly-stained cells of the apical initial group, the surface cells on the flanks of the apex are smaller and stain

more deeply with safranin (Plate 25, figs. 1, 2; Plate 27, figs. 1, 2). In this respect, they are identical with the cells of the inner peripheral layers and hence are regarded as an integral part of Zone IV (cf. fig. 3).

CENTRAL MOTHER CELLS (*Zone II, fig. 3*)

In spite of their position in the upper central region of the shoot apex, the central mother cells have none of the characteristics usually associated with the primordial meristem of seed plants (Priestley 1928, 1929). In the first place, they are the largest cells of the apical meristem, often reaching a maximum length of 30–35 microns and a width of 15–20 microns; the cells of the peripheral layers and of the "transition zone" in contrast average $\frac{1}{2}$ to $\frac{1}{3}$ these dimensions. The "enucleated" appearance of certain of the central mother cells shown in Plate 26, figs. 1 and 2 illustrates how, in such large cells, the plane of a thin section may be above or below the level of the nucleus. Secondly, the central mother cells are sharply demarcated from the neighboring peripheral layers (Zone IV) by their larger, more lightly stained nuclei and by the less dense and more vacuolated appearance of their cytoplasm (Plates 25–27). Indeed, from a purely cytological standpoint, the zone of central mother cells bears a marked resemblance to the young apical-cell segments typical of certain vascular cryptogams (Kaplan 1937 p. 229, Zirkle 1932 p. 32). Admittedly, however, the present study is limited to a description of appearances obtained when meristem is killed and fixed in formalin-acetic acid-alcohol and stained in safranin. A further study of the whole problem therefore with the use of a wide range of killing reagents (Zirkle 1932) and stains (Vidal 1912), would certainly be profitable.

Although mitoses have been observed in the central mother cells (figs. 7b, 8, 9; Plate 26, fig. 1; Plate 27, fig. 2) they are noticeably less frequent than is true of the cells of Zones IV and V. Furthermore, indirect evidence of the reduced mitotic activity of the central mother cells is furnished by their relatively large size and by the lightly stained appearance of their nuclei. These facts suggest that, unlike the situation in the primordial meristem of angiosperms, cell enlargement rather than cell division is the dominant aspect of growth in the central mother cells.

As indicated by the highly irregular arrangement of cells, ***growth in volume*** is typical of the zone of central mother cells, which thus agrees, at least in this respect, with the corpus region of the angiospermous growing point.[3] A careful examination of longitudinal and transverse series shows that no regular plan of segmentation is followed by the central

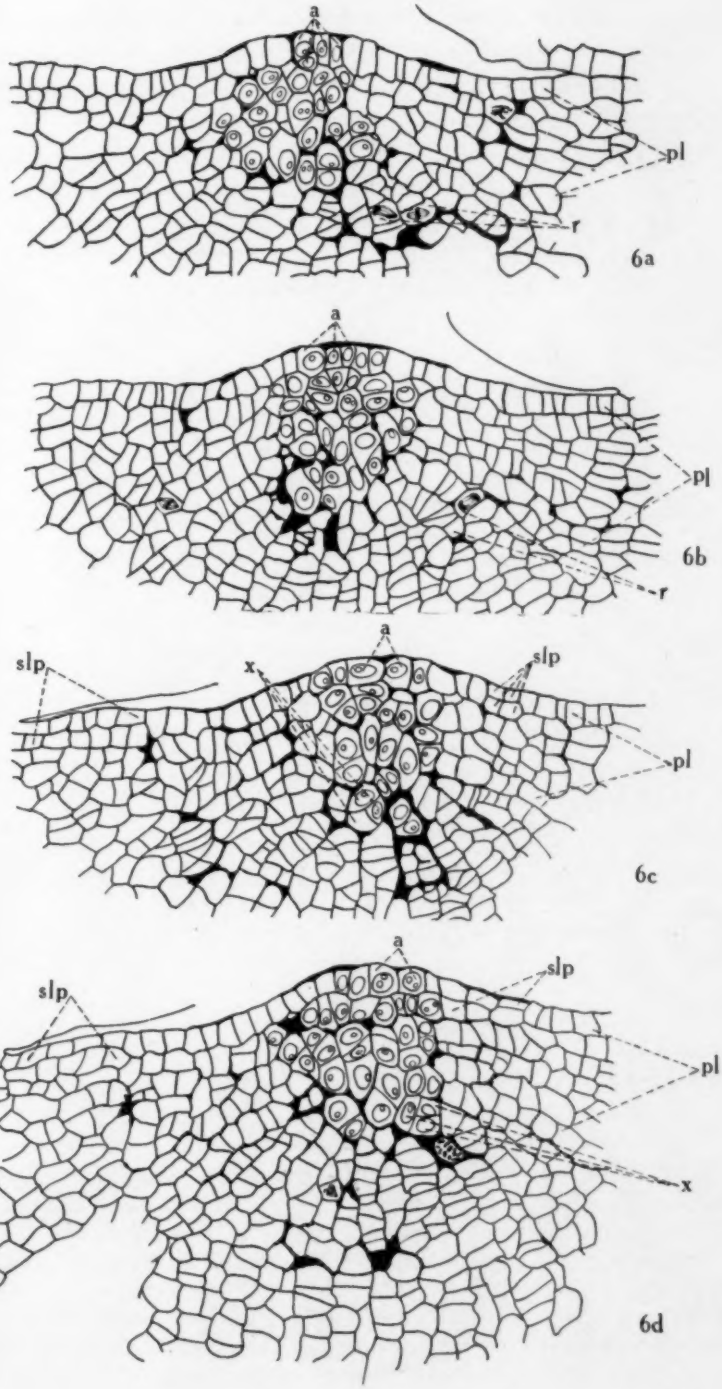
[3] For details regarding the tunica-corpus zones of the shoot apex in angiosperms cf. Schmidt (1924), Priestley (1928, 1929), Foster (1935, 1936, 1937), Cross (1936, 1937, 1938), Newman (1936), Kliem (1937).

mother cells. Nevertheless, there is a marked tendency for the cells, especially in the "axial" region, to divide periclinally in respect to the surface of the shoot apex (figs. 6b, 6c, 6d, 8, 9, 12; Plate 25, fig. 1; Plate 27, figs. 1, 2). Following such divisions, either or both of the daughter cells may divide anticlinally (figs. 6c, 6d, 7a, 10, 11; Plate 27, figs. 1, 2). In this way, new cells are continually formed toward the peripheral and basal regions of the zone. However, the wall-bending and unequal enlargement of all cells, as well as frequent obliquities in the insertion of new walls are facts which preclude any exact determination of cell lineages. Consequently, it seems reasonable to conclude that fluctuations in the rate and directions of growth within the "plastic" mass of central mother cells determine the cell pattern at any given point, rather than any inherent sequence of cleavages.

A very puzzling but constant feature of the central mother cells is the irregular and often massive "thickenings" which appear at the corners or along the sides of many of the cells (figs. 5–12; Plates 25–27). Although a detailed physical-chemical investigation has not been made, these "thickenings" seem to represent localized deposits of intercellular substance together with unusually thickened areas in the primary wall.[4] As is shown in figs. 6d, 7a, 7b, 11, and 12, these depositions frequently resemble very strikingly the "corner thickenings" typical of many collenchyma cells. Occasionally, in longitudinal sections, a surface view is obtained of the entire lateral wall of a central mother cell. From this aspect, the wall thickening appears as an irregular reticulum the meshes of which closely resemble simple pits (Plate 25, fig. 2). It is significant that thickened areas, apparently identical to those in the central mother cells, occur sporadically in other zones of the shoot apex, and serve to delimit cell groups of common origin. This is very obvious at the points of origin of the rib meristem from the base of the transition zone (figs. 6a, 6c, 6d, 7a, 7b, 12; Plates 25, 27).

[4] The terms "intercellular substance" and "primary wall" are used in the sense recently defined by Kerr and Bailey (1934).

Figs. 6a–6d. Successive longisections, at intervals of 14 microns, through the apex of a spur shoot, illustrating the prominence and clear demarcation of the zone of central mother cells and the origin, mode of growth and planes of division of the cells of the peripheral layers and the rib meristem in various regions of the apex. Fig. 6c is approximately median. Note especially the periclinal divisions which have occurred at various points in the surface layer and the characteristically irregular arrangement of the central mother cells. T divisions, associated with the origin of the rib meristem, are shown in the cell groups labeled X in figs. 6c and 6d.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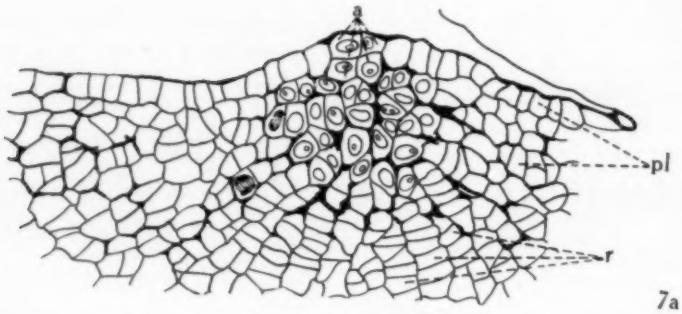

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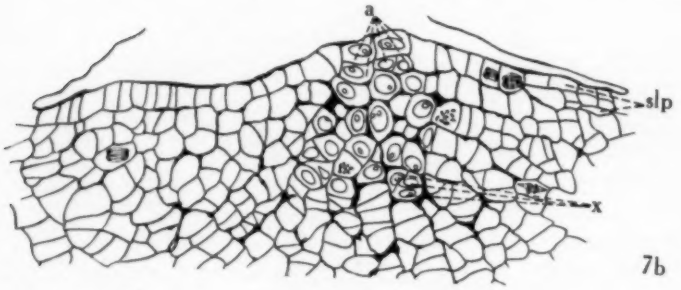

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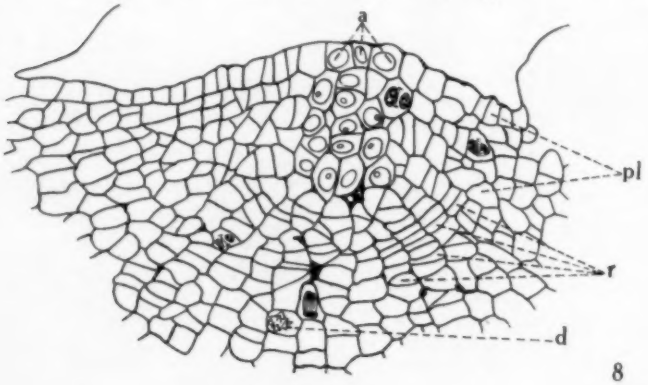

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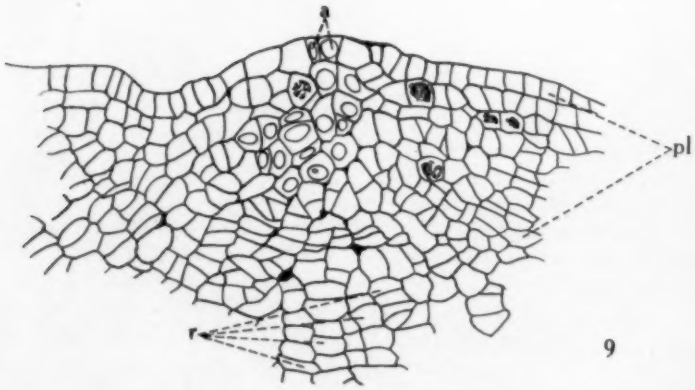

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The gradual disappearance of the "thickenings" in the distal regions of the shoot apex suggests that they may experience "reversible" changes during tissue differentiation.

THE PERIPHERAL LAYERS (*Zone IV, fig. 3*)

The expression "peripheral layers" designates a well-defined zone composed of several layers of small, densely cytoplasmic cells. A comparison of transverse and median longisections demonstrates that this zone occupies the flanks of the shoot apex and hence completely surrounds the central mother cells (Plate 26, figs. 1, 2). It should be evident, therefore, that in longisections which pass through the sides, rather than the center of the growing point, a definitely stratified arrangement of cells would be seen. Fankhauser's (1884, taf. II, figs. 7–8) failure to observe the zone of central mother cells and his depiction of "periblem" layers would thus appear to depend upon a study of sections cut in this plane. A similar criticism of the statements of Strasburger (1872) in regard to "histogens" in *Ginkgo* seems justifiable.

From a cytological standpoint, all the cells of the peripheral layers are similar in appearance and, in respect to their small size, deeply stained protoplasts and frequent divisions, correspond to typical primordial meristem. This marked uniformity in structure is interesting in view of the difference in point of origin of the various layers. The outermost or truly surface layer, as I have shown, arises from the apical initial group but by sporadic periclinal divisions undoubtedly augments the subsurface layer (figs. 6c, 6d, 7b, 10; Plate 25, fig. 2). In contrast, the inner cell layers have a separate and independent origin. As is shown in Plates 25 and 27, these layers are continually augmented by the division of the cells at the upper periphery of the zone of central mother cells. In terms of cell activity, this peripheral region truly represents a transition zone between an area of cell enlargement (i.e. the zone of central mother cells) and a region characterized by pronounced meristematic features. From this point of view,

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Figs. 7a–7b. Longisections through the apex of a spur shoot; Fig. 7a approximately median, Fig. 7b 35 microns distal to Fig. 7a. Both figures illustrate the origin of new central method cells from the inner derivatives of the apical initial group. Note in Fig. 7a the clear demarcation of the U-shaped "transition zone" and in Fig. 7b, a typical T division at X.

Fig. 8. Median longisection through the apex of a spur shoot. Note the anticlinal telophase in one of the central mother cells and the clear definition of the U-shaped transition zone.

Fig. 9. Median longisection through the apex of a spur shoot, illustrating, at the right, anticlinal divisions in several cells of the peripheral layers. Note the polar view of chromosomes in one of the central mother cells.

the central mother cells in *Ginkgo* resemble the situation in the apical meristem of many cryptogams where a zone of large initials merges abruptly into a zone of smaller, dividing cells (cf. Schüepp 1926 p. 6–7). Although it is evident that the sequences of division are variable in the transition zone, transverse sections show that the most recently formed cells are arranged in short radial rows which collectively simulate a cambium (Plate 26, figs. 1, 2). This definitely indicates that the new walls tend to be anticlinal or anticlinal-oblique with reference to the flanks of the shoot apex (figs. 5, 6b, 7a, 8, 11, 12, Plates 25, 27).

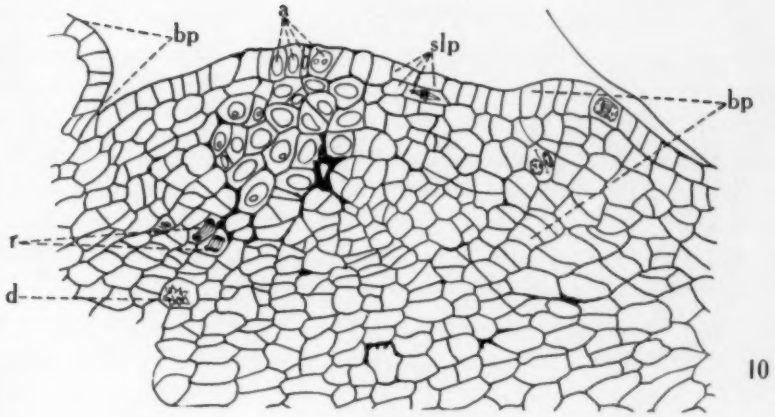
Although surface growth is dominant in the zone of peripheral layers (cf. figs. 3, 8, 9) many irregularities in the cell net are produced by periclinal or oblique divisions. Consequently, the peripheral layers show none of the regularity of growth and independence characteristic of the tunica region of the shoot tip in angiosperms (Schmidt 1924). Their closest resemblance is clearly with the outer meristematic layers found in the shoot apices of conifers (Koch 1891, Korody 1937) and certain species of *Lycopodium* (Härtel 1938). Furthermore, as in the forms just named, the regularity of the peripheral layers is noticeably disturbed by the initiation of bud scales and foliage leaves. The inception of these organs is always associated with a local increase in the frequency of periclinal divisions (figs. 5, 10). Frequently, although not invariably, foliar initiation involves the periclinal divisions of the surface layer itself (fig. 5).

In terms of differentiation, the outer surface layer produces the epidermal system of the shoot while the cortex arises from the inner peripheral layers. Vascular differentiation has not been followed in this investigation but there is evidence that the meristem ring (Barthelmess 1935 p. 214 fig. 5) and hence ultimately the procambium, originates from the innermost layer or layers of Zone IV (cf. fig. 5).

Fig. 10. Median longisection through the apex of a spur shoot, illustrating at the right the origin of a bud scale primordium from the zone of peripheral layers. The presence of a druse in a cell of the rib meristem at the left is indicative of the abrupt differentiation of the broad pith characteristic of spur shoots.

Fig. 11. Median longisection through the apex of a spur shoot, showing an exceptionally prominent trio of apical initials, from which by anticlinal and periclinal divisions, new surface and internal segments have arisen.

Fig. 12. Median longisection through the apex of a spur shoot, showing clearly the irregular size, shape and mode of segmentation typical of the central mother cells. Note the well defined position of the transition zone in this preparation and the clear rib meristem.



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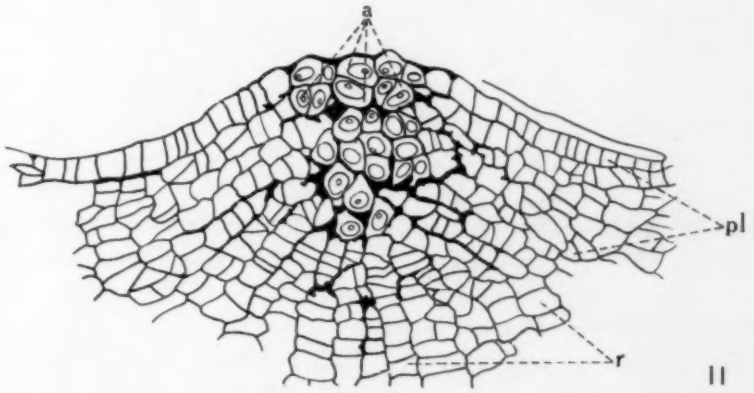

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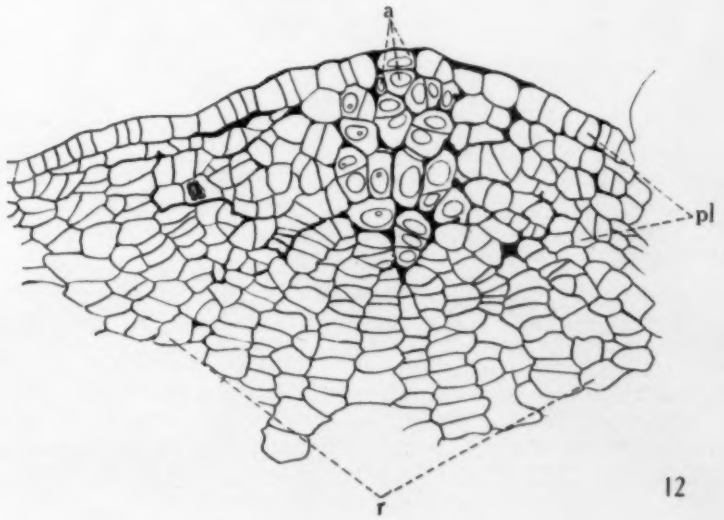


12

THE RIB MERISTEM (*Zone V, fig. 3*)

The term "rib meristem" has been devised by Schüepp (1926 pp. 18–19) to designate a type of primary meristem which is responsible for the *growth in length* of young internodes, roots, and the petioles of leaves. Growth in a longitudinal direction prevails in the rib meristem and this tissue consists of vertical series of genetically-related cells which have been formed by repeated transverse (i.e. anticlinal) divisions. Although the entire pith region of a shoot axis is produced by rib meristem, interesting differences exist in regard to the point of origin of this meristem in seed plants. In the dicotyledons, the rib meristem forming the pith originates some distance from the surface of the growing point by the active division of the cells of the corpus (Foster 1935, Cross 1936, 1937). In many conifers however, the pith of the shoot axis differentiates far in advance of the other primary tissues and the rib meristem appears as a central core of vacuolating cells which arises *directly* from the inner embryonic layers of the growing point[5] (Koch 1891, Korody 1937). Obviously in both types, the origin of the rib meristem is associated with a more or less abrupt transition from highly meristematic to vacuolating and "stretching" tissue. In *Ginkgo* just the reverse condition occurs since here the transition to rib meristem first involves the *renewal* of mitotic activity in the lower central mother cells. As is true of the origin of the inner peripheral layers, this renewed mitotic activity is accompanied by a decrease in cell size and a greater retention of the nuclear stain (Plates 25, 27).

[5] This fact has been confirmed by the writer in a brief unpublished study of the shoot apex of *Abies venusta*. (Dougl.) K. Koch.

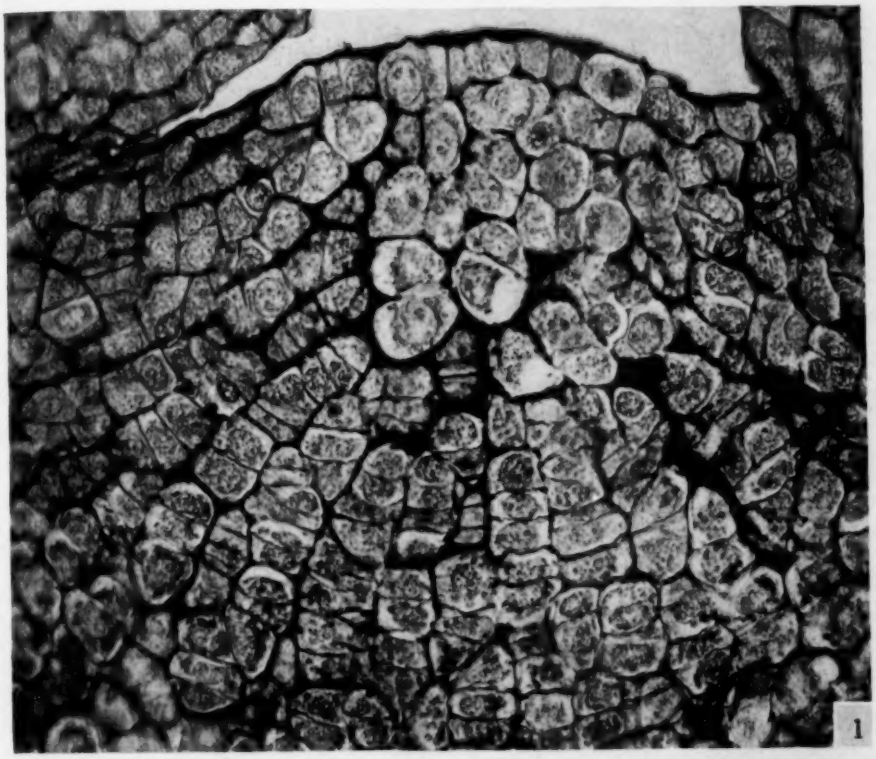
Explanation of plates

(*all figures* ×*435*)

PLATE 25

Fig. 1. Median longisection illustrating the zonal structure typical of the apex of a spur shoot (April 15). The zone of central mother cells, seen in the upper center directly beneath the apical initials, is sharply demarcated from the peripheral layers and the basal zone of rib meristem by the large size, irregular arrangement and lighter-stained appearance of its cells. Note the prominent "wall-thickenings" (stained black) both in the zone of central mother cells as well as in the surrounding zones. An anticlinal metaphase is evident in a cell of the surface layer at the right. The short vertical extent of the rib meristem in this shoot is shown at lower magnification in Text Fig. 1.

Fig. 2. A similar longisection of a spur shoot (April 29). Note especially that the surface layer, on both flanks of the apex, has divided periclinally. To the left and slightly above the prominent metaphase in a cell of the rib meristem, will be seen in surface view the "reticulate" or "pitted" character of the lateral wall of a central mother cell. Note, as in Fig. 1, the rapid maturation of the pith from the short zone of rib meristem.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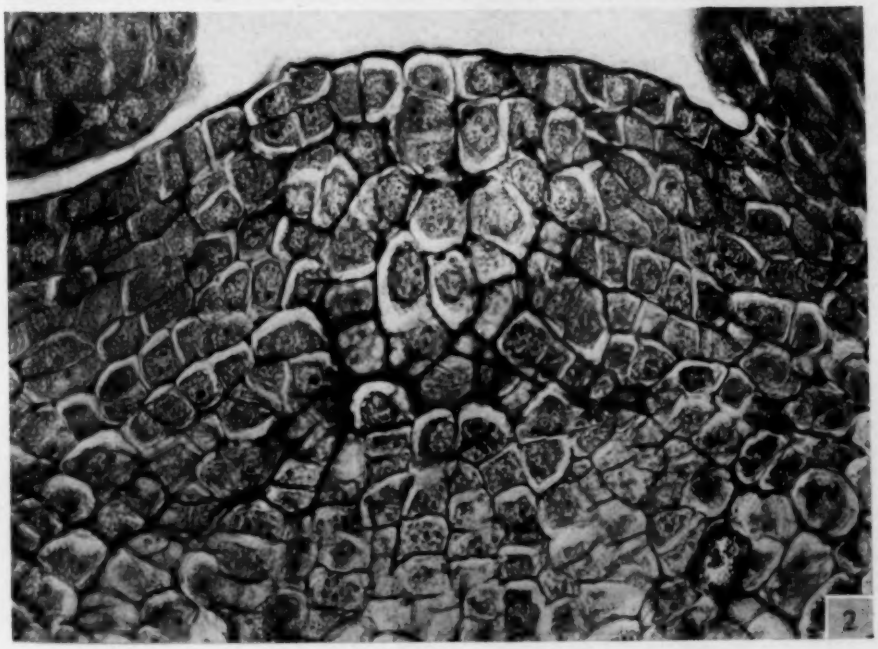
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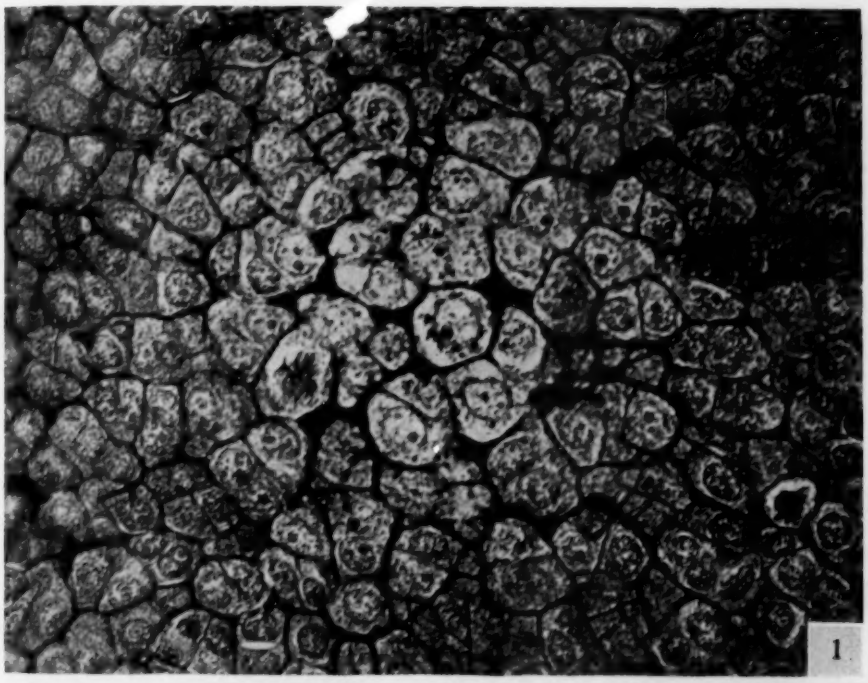
As seen in median longisection, the transition zone giving rise to the young rib meristem appears as a concave area of small, tabular frequently-dividing cells (cf. especially figs. 5, 6b, 7a, 8, 10, 11, 12 and Plates 25 and 27). The well demarcated appearance of this formative region is the result of the early prevalence of periclinal or periclinal-oblique divisions. Frequently, the repeated formation of periclinal walls in several adjacent cells produces regular short filaments of genetically-related cells (figs. 5, 7a, 10). Often however, following the first periclinal or oblique division, the lower daughter cell divides anticlinally thus giving rise to a double series of cells. Such T divisions are illustrated in Figs. 6c, 6d, and 7b by the label X. As noted previously, the wall thickenings of the central mother cells may be "carried over" into the zone of rib meristem and thus aid in the identification of cell groups of common lineage (figs. 6a–6d, 7a–7b, 10, 11, 12; Plates 25, 27).

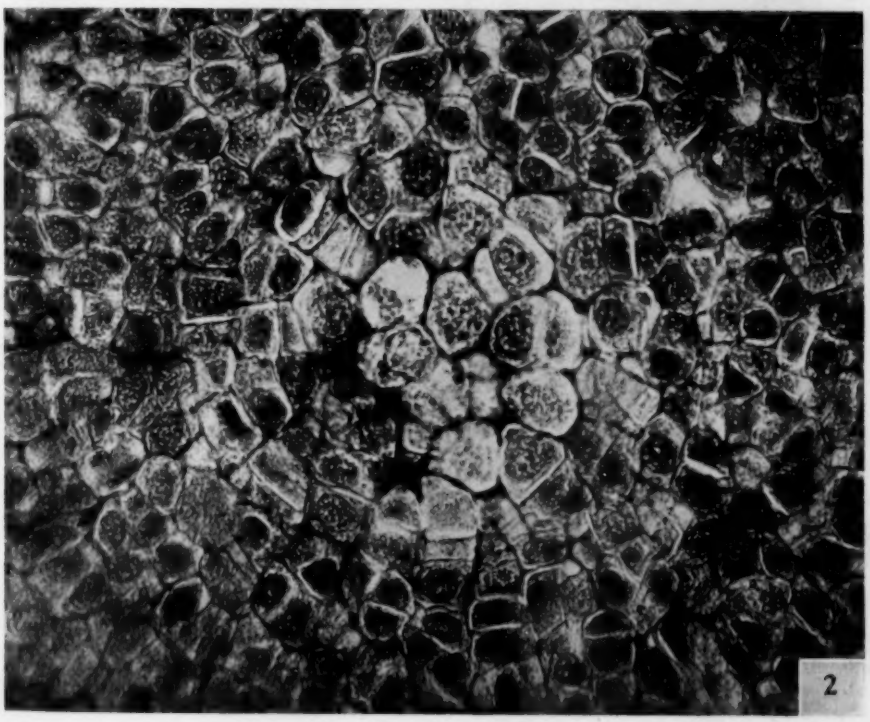
Although the prevailing direction of growth in the young rib meristem is periclinal in respect to the surface of the shoot axis, irregularities in the cell pattern are common and result from periclinal or oblique division of cells at various points. In this way, new chains of cells are formed which appear to "insert" themselves (possibly by "gliding growth") between their neighbors (figs. 6b, 6c, 6d, 7a, 12; Plate 25, fig. 1; Plate 27, fig. 2). A marked difference, which has already been noted, occurs in respect to the duration and mode of growth of the rib meristem in long and spur shoots. In the latter, the rib meristem looses its embryonic character a short distance from the zone of central mother cells and abruptly differentiates into the broad, radially-expanding pith region (fig. 1). Associated with this early cessation of growth, druses frequently appear in many of the cells of the maturing rib meristem (figs. 5, 8, 10). In long shoots however, the rib meristem retains its capacity for growth and cell division for a much longer period of time, and together with the equally active rib meristem beneath the epidermis, makes possible the formation of elongated internodes (fig. 2;

Explanation of Plate 26

Fig. 1. Transverse section of the apex of a spur shoot (April 15) 63 microns below the apical initial group, showing that the large central mother cells (note metaphase) are completely surrounded by the smaller more densely-stained cells of the peripheral layers. The cells of the transition zone, at the margin of the central mother cells, are arranged in irregular radial rows. Compare with Plate 25, figs. 1 and 2.

Fig. 2. Transverse section of the apex of a spur shoot (May 11), 63 microns below the apical initial group depicted in text figure 4. The prominent lightly-stained central mother cells are surrounded by a "cambial-like" transition zone showing a marked radial alignment of cells. Note the anticlinal telophase in one of the cells at the right, and the mitosis in a cell of the peripheral layer at the lower left.





FOSTER: GINKGO

Plate 27, figs. 1, 2). Indeed the unusually active rib meristem in the long shoots of *Ginkgo* would provide excellent material for a study of the rhythmical aspects of mitosis along the lines suggested by the recent investigations of Wagner (1930, 1937).

DISCUSSION

From a comparative anatomical standpoint, the shoot apex of *Gingko* exhibits a type of structure which, in the light of present knowledge, appears unique among vascular plants. On the one hand, it diverges from such vascular cryptogams as *Equisetum* (Vidal 1912) and the leptosporangiate ferns (Bower 1889) in the absence of a definite apical cell and the highly variable sequence of cleavages throughout the meristem. The peculiar cytological features of the apical initials and the central mother cells in *Ginkgo* are, it is true, suggestive of the condition described by Hof (1898) for the apical region of the root of *Pteris*, and for the shoot tip of Osmunda (Zirkle 1932, pp. 32–36) but the resemblances are clearly "physiological" rather than "morphological." Furthermore, although such plants as *Lycopodium* (Schüepp 1926 pp. 48–49, Härtel 1938) and the Marratiaceous genera *Danaea* and *Kaulfussia* (West 1917) agree with *Ginkgo* in the possession of a single tier of apical initials, they differ markedly in the zonal arrangement of their meristems. On the other hand, *Ginkgo* shows but few points of histological similarity with the shoot apices of other gymnosperms. Possibly the closest comparison can be drawn with the Abietaceae which resemble *Ginkgo* in the form and behavior of the apical initials and especially in the absence of a typical "dermatogen" (Koch 1891, Korody

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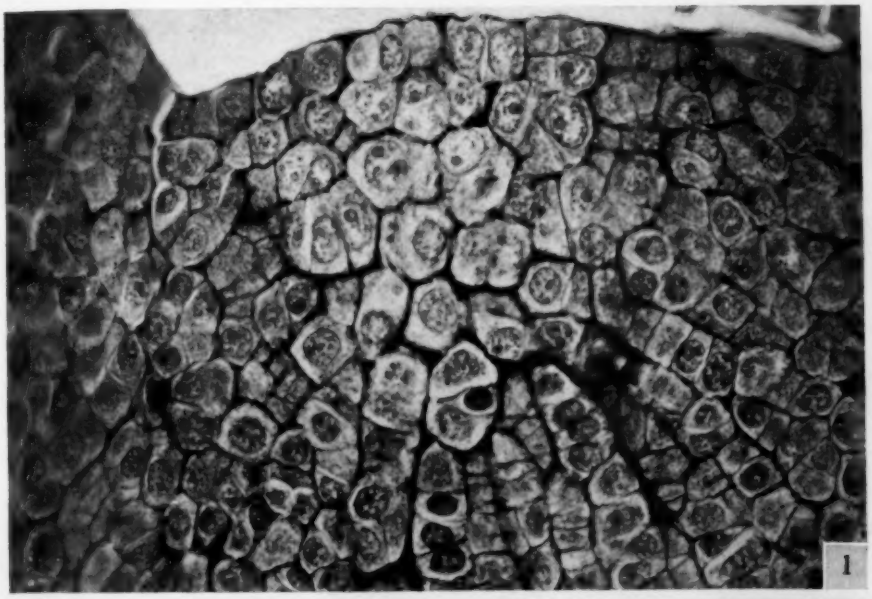
Explanation of Plate 27

Fig. 1. Longisection showing the details of structure of the apex of the long shoot illustrated in text figure 2. Note the marked contrast between the large, lightly-stained central mother cells (upper center of figure) and the smaller cells of the peripheral layers and the rib meristem. At the right of the apical initial group will be seen a quartet of cells produced by the "decussate" division of a surface segment. As in the apices of spur shoots (Plates 25 and 26) irregular "wall thickenings" are evident in the zone of central mother cells and help to define genetically-related cell groups in the rib meristem.

Fig. 2. Longisection illustrating the characteristic structure, mode of growth and planes of cell division in the various zones of the apex of a long shoot (April 22). Note the recent periclinal division in a cell of the apical initial group and the anticlinal metaphase in a surface segment at the right. The periclinal division of the surface layer is evident on each flank of the apex. Mitoses are also shown in a central mother cell (upper left) and in cells of the peripheral layers (upper right). Note especially the active propagation of the filamentous groups of rib meristem from the basal margins of the zone of central mother cells.



FOSTER· GINKGO

1937). However, the well-defined zone of central mother cells is peculiar to *Ginkgo* and, as far as I am aware, is not duplicated in the shoot tips of the conifers. In the latter, according to the classical investigations of Koch (1891), the meristem is arranged in two zones which are clearly defined as to cell structure and mode of growth, viz.: (1) an outer "Hüllgewebe" composed of several layers of typical meristematic cells which produce the epidermis, cortex, procambium and foliar organs and (2) an inner core or "central tissue" of somewhat vacuolated cells which form the pith. It is clear from Koch's descriptions and excellent drawings that unlike the condition in *Ginkgo*, the rib meristem (i.e. his "central tissue") in the shoot apices of conifers is propagated directly from a small subterminal group of "mother cells." The latter, except in their position and predominant periclinal division, resemble in size, form and dense cytoplasm the neighboring cells of the "Hüllgewebe" and hence show none of the definitive characteristics of the central mother cells of *Ginkgo* (cf. Plates 25–27). Koch's observations have been confirmed in a recent study by Korody (1937) for the shoot tips of *Abies*, *Picea* and *Pinus*. This investigator makes a sharp distinction between the "Bildungselement" (i.e. the "corpul-like" terminal region of the apex) and the "Strukturelemente" (i.e. the embryonic layers and the central tissue) in the growing point. Her descriptions, drawings and photomicrographs again emphasize that the "mother cells," from which the two "structural elements" are propagated, are not comparable either in extent or histological features to the central mother cells of *Ginkgo*. On comparative grounds it is interesting to note that Härtel (1938 pp. 165–166) finds a marked resemblance between the general structure and growth of the shoot apex in the conifers and that typical of various species of *Lycopodium*. In the latter however, only the subapical "mother cells" are polygonal in form and the "central tissue" arising from them consists of small elongated spindle-shaped cells which differentiate into the vascular tissue of the protostele.

In view of the archaic and probably primitive morphology of *Ginkgo*, it would be tempting to argue that the distinctive structural features of its shoot apex typify a "primitive stage" in the evolution of the apical meristem of seed plants. For the present however, a rather conservative viewpoint seems preferable because of the debatable relationship between *Ginkgo*, the conifers and the flowering plants (cf. Sprecher 1907 p. 198) and Chamberlain (1935 p. 433–436) and particularly because our knowledge of the comparative anatomy of apical meristems in the spermatophytes is still very meagre. Strasburger (1872) and Schüepp (1926 pp. 50 and 55) have both suggested that the architecture of the shoot apex in gymnosperms serves to articulate the condition found in *Lycopodium* with

that typical of angiosperms. Indeed in *Araucaria* according to Strasburger (1872, taf. XXIII, fig. 13) the outer surface layers of the shoot correspond in mode of arrangement to Hanstein's (1868) "dermatogen" and "periblem" and hence resemble the tunica zone of a dicotyledon. Nevertheless our present knowledge seems insufficient to deduce with confidence the phylogenetic development of the stratified condition of the apical meristem typical of the angiosperms. Korody (1937) has approached the problem from the theoretical standpoint advanced by Buder (1928). She maintains that because of the single tier of apical initials in *Abies*, *Picea* and *Pinus*, the entire apical meristem may be homologized with the corpus region of the shoot apex in angiosperms. A similar conclusion is reached for *Lycopodium* by Härtel (1938). I cannot agree with this interesting theory however, because it is based upon too rigid a morphological distinction. In my opinion, tunica and corpus represent *interdependent growth zones* in an apical meristem and as such, one cannot exist independently of the other. Consequently, in agreement with Schüepp (1926, 1927) I would regard the condition in the Abietaceae as indicative of a transitional stage in the evolution of the zonation typical of the shoot tip in angiosperms. From this viewpoint, it may subsequently prove correct to interpret the structural pattern in *Ginkgo* as an even lower stage in the evolutionary sequence.

In conclusion, it seems fitting to emphasize the need for a complete re-examination, along broad comparative lines, of the architecture and modes of growth of the shoot apex in gymnosperms. It would be particularly interesting to explore the situation in the cycads, since they play such an important rôle in evolutionary theory. The older literature dealing with the apical meristem in gymnosperms seems to have dealt largely with the question of the existence of an apical cell (for resumés of the literature cf. Koch 1891, Schüepp 1926 and Korody 1937). However, the recent studies of Helm (1932), Louis (1935), Barthelmess (1935) and Kaplan (1937) indicate the increasing tendency to emphasize the behavior of *entire cell complexes* during embryonic growth and differentiation, rather than the "destiny" of individual cells. This attitude has guided the present investigation and if consistently applied in comparative studies should increase our understanding of the fundamental interrelationship between growth and structure in the shoot apex of vascular plants.

SUMMARY

The meristem of the apex of spur and long shoots in *Ginkgo* is not uniform in structure but is segregated into five distinctive zones characterized by the size, staining reactions and mode of growth of the component cells.

The uppermost zone is represented by the apical initial group, from which by anticlinal and periclinal divisions respectively, the surface layer and the internal cells of the shoot apex originate. There is no regular sequence in the successive planes of division of the cells of the apical initial group, and the cell net is correspondingly variable in pattern. Furthermore, periclinal divisions are not restricted to the apical initials but occur at any point in the surface layer.

Directly beneath the apical initial group is found the zone of central mother cells which constitutes the most unique feature of the shoot apex. In their large size, irregular arrangement, relatively infrequent divisions and lightly stained protoplasts, the central mother cells diverge from the structural features usually associated with the primordial meristem of seed plants. It is concluded that volume growth predominates in this zone which, in this respect, is analogous to the corpus region of the angiospermous growing point. A puzzling feature of the central mother cells is the presence of thickened areas at the corners or along the sides of many cells or cell groups. These thickenings are provisionally interpreted as local and temporary depositions of intercellular and primary wall substance.

The lateral and basal margins of the central mother cells represent a "transition zone" from which, by means of renewed mitotic activity, are propagated respectively the bulk of the zone of peripheral layers and the zone of rib meristem.

The zone of peripheral layers, because of the small, deeply stained frequently dividing cells which compose it and the notable emphasis on surface growth might be compared with the tunica region of the growing point in angiosperms. However, periclinal divisions may occur at any point so that there is no constancy in the number of cell layers. In terms of differentiation, the epidermis, cortex and procambium of the shoot axis arise respectively from the outer, middle and innermost of the peripheral layers.

The zone of rib meristem consists of short chains of cells in which growth in length and transverse divisions predominate. The number of filamentous series is continually augmented by periclinal or oblique divisions. In the spur shoot, the closely crowded internodes result from the limited period of activity of the rib meristem which, a short distance from the growing point, gives rise to the broad rapidly maturing pith. By contrast, internodal extension in the long shoot is related to the much greater capacity for continued growth and cell division in the rib meristem of both pith and cortical regions.

The shoot apex of *Ginkgo* possesses a unique type of structure which is not duplicated in vascular cryptogams or seed plants. It is suggested that in some respects however it may typify a "primitive stage" in the evolu-

tionary development of the tunica-corpus regions typical of the shoot apex in angiosperms.

UNIVERSITY OF CALIFORNIA,
BERKELEY

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Some New and Interesting Late Tertiary Plants from Sucker Creek, Idaho-Oregon Boundary*

HELEN V. SMITH

(WITH PLATES 28 AND 29)

In this paper are descriptions of six new species and records of seven species not previously reported from Sucker (i.e., Succor) Creek. Sucker Creek is mostly in Malheur County, southeastern Oregon, and flows in a northerly direction near the Idaho-Oregon boundary line finally crossing into Owyhee County, Idaho, where it empties in the Snake River.

Collections were made from the Miocene lake beds during the summers of 1931, 1932, 1934, and 1936 from three principal localities. In the lower part of the valley specimens were obtained from several beds close to the old Ballantyne Ranch house in Idaho and two or three miles farther up the creek near an old coal prospect. In the upper part of the valley the collections were made from several beds within three or four miles of the Rockville, Oregon, postoffice. There do not appear to be any notable variations among the fossils of the same species collected at the various localities, and the plant associations represented are apparently the same and of the same age. However, the specific localities for the new species are reported here since more extensive studies may eventually indicate locality variation in the florula.

DESCRIPTION OF SPECIES

Polypodiaceae

Woodwardia deflexipinna n. sp. (Plate 28, figs. 3, 6). Outline of frond unknown; pinnae lanceolate; sterile and fertile pinnae alike; pinnae cut three fourths of the distance to the midrib; pinnules broadly lanceolate, rounded at the apex, broadest at base, 1 cm. long, not auricled; margin entire and slightly revolute in some specimens; mid-vein of pinnae and pinnules with a single series of oblong, very slightly oblique areoles on each side; outer veins free, ending along the margin; sori linear or oblong, one to each aerole.—Type, no. 20014, Mus. Paleont., Univ. of Mich. Collected near Rockville, along the Strode Ranch road east of the postoffice.

The living species to which this fossil seems to be most closely allied is *Woodwardia virginica* (L.) Smith (Plate 28, fig. 2), the common chain fern of eastern North America. In venation, size and distribution of the sori, the entire margin, and rather spreading pinnae the two forms are practically identical.

Among the eight fossil species of *Woodwardia* from the western states this is closest to *W. Maxoni* Knowlt. and *W. crenata* Knowlt. from the

* Papers from the Department of Botany of the University of Michigan no. 661.

Eocene. The Sucker Creek species differs from these particularly by having an entire instead of serrate margin and in the smaller size of the pinnules.

At one locality on the east side of the valley near Rockville, Oregon, this species is extremely abundant. A ledge several inches thick is a mass of fern fragments and many immature rolled up fronds are also common.

Equisetaceae

Equisetum octangulatum n. sp. (Plate 28, fig. 1). Stem 4.5 mm. wide; internode 3.3 cm. long; 4 or 5 longitudinal ribs visible; 5 small branch scars, and no leaves visible at the node.—Type, no. 20013 Mus. Paleont., Univ. of Mich. Collected near the Ballantyne Ranch.

The fragment figured here is the only well preserved specimen in the collection. In spite of its poor representation it seems to be advisable to report the species.

Pinaceae

Pinus sp. (Plate 28, fig. 8). Needles short, in groups of three; rigid; slender, sharply pointed; 2.7 cm. long.

These needles differ from those assigned to *P. Knowltoni* Chaney (3) in being more rigid, narrower, and considerably shorter. They are very straight and not curved as they often are in *P. Knowltoni*.

The short *Pinus* needles from Salmon, Idaho, figured by Brown (1) in Plate 45, fig. 10 may represent the same species.

Betulaceae

Betula Bendirei Knowlt. (Plate 29, fig. 3). The single specimen referred to this species is practically identical with leaves of the living *B. occidenta-*

Explanation of Plate 28

Fig. 1. *Equisetum octangulatum* H. V. Smith. Type; Mus. Paleont., Univ. of Mich. no. 20013.

Fig. 2. *Woodwardia virginica* (L.) Smith. Specimen from Bloomfield, Michigan in the Herbarium, Univ. of Mich.

Fig. 3. *Woodwardia deflexipinna* H. V. Smith, Type; Mus. Paleont., Univ. of Mich. no. 20014.

Fig. 4. *Acer Buergerianum* Miq. Specimen from the Botanical Gardens, Univ. of Mich.

Fig. 5. *Acer Bolanderi* Lesq.

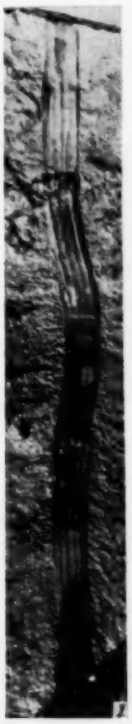
Fig. 6. *Woodwardia deflexipinna* H. V. Smith. Fertile pinnule.

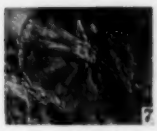
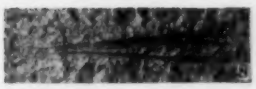
Fig. 7. *Dipteronia insignis* (Lesq.) R. W. Brown.

Fig. 8. *Pinus sp.*

Fig. 9. *Nyssa aquatica* L. Specimen from Richland Co., Ohio in Herbarium, Univ. of Mich.

Fig. 10. *Nyssa oregonensis* H. V. Smith. Type; Mus. Paleont., Univ. of Mich. no. 20015.



lis Hook. This living species occurs along the borders of streams, and margins of meadows in rich moist humous, sandy, and rocky soils. It is found from southwestern British Columbia to northern Washington and east to the Rocky Mountains.

Among fossil species this seems to be most similar to *B. lacustris* MacG. from Trout Creek, Oregon. The Trout Creek species is closely related to *B. fontinalis* Sarg. which was long confused with *B. occidentalis*.

Although the specimen in this collection does not correspond exactly with that figured by Knowlton (4), it is referred to his species because of its resemblance to *B. occidentalis* which he considered to be similar to his fossil. It also answers to Knowlton's description.

Fagaceae

Quercus malheurensis n. sp. (Plate 29, fig. 1). Leaves subcoriaceous, rather small, length up to 7 cm. (estimated), width to 4.5 or 5 cm.; sparsely lobed; lobes rounded, not bristle tipped, one or two on each side of leaf, the lower much larger than the upper; apex of leaf broadly rounded; base cuneate; midrib and lateral veins strong, somewhat undulate; principal lateral veins extending to the tips of the lobes; smaller veins opposite or alternate, relatively weak, curving upward in an irregular manner and becoming effaced; tertiary venation not visible; ultimate venation a fine regular reticulum.—Type, no. 20010 Mus. Paleont., Univ. of Mich. Collected near the old Ballantyne Ranch house.

These leaves belong to the white oak group and resemble some of the sparsely lobed small leaves of *Q. alba* L. They differ from previously figured fossil oaks of this group chiefly in the small number of lobes and small size, and when a larger series of specimens becomes available may be found to represent a small form of some previously described species. For the present, however, it would be merely guessing to place this fossil with any described form, and there would be the great disadvantage that it might lead to confusion in the record of the other species to which it was referred.

Rutaceae

Ptelea enervosa n. sp. (Plate 29, fig. 6). Samara almost round, winged all around, 2 seeded; seed cavity 4 mm. wide, 6 mm. long; total length of samara 1.7 cm.; total width 1.8 cm.; wing firm, with no visible venation.—Type, no. 20011, Mus. Paleont., Univ. of Mich. Collected near the old Ballantyne Ranch.

A single samara was found in the lower Sucker Creek Valley. It is readily distinguishable from *P. miocenica* Berry by its smaller size and the firm wing with no visible venation. Among living forms examined this is closest to *P. mollis* M. A. Curtis var. *cryptoneura* Bartlett (Plate 29, fig. 7). The living plant has samaras of the same size and shape and the veins are

likewise very indistinct. It occurs in the southeastern states. No leaves referable to *Ptelea* have been observed in the collection.

Anacardiaceae

Rhus oregonensis n. sp. (Plate 29, fig. 9). Leaf membranaceous, 4.5 cm. wide, 6.5 cm. long; palmately deeply three-lobed or compounded; leaflets pinnate; terminal leaflet broadest just below the middle, tapering cuneately below and having two pairs of small rounded lobes or teeth above; apex apparently acuminate; lateral leaflets with three lobes above and four below, the basal inferior lobes of each lateral leaflet much larger, quite distinct and extending downward; secondary veins enter the shallowly toothed lobes; tertiary venation obsolete; sinuses between the three main lobes very narrow.—Type, no. 20012 Mus. Paleont., Univ. of Mich., collected near Rockville, Oregon.

The leaf was compared with specimens of three genera that may have leaves of this general type; *Acer*, *Panax*, and *Rhus*. Superficially similar leaf forms are found in *P. trifolium* L. and *P. quinquefolium* L. The differences are rather marked, neither has the small prominent basal lobe, the former has smaller more numerous marginal teeth and the latter has much narrower lobes than the fossil. As these are both low-growing herbaceous forms the chances of anything related to them entering the fossil record would be extremely slight. Various deeply dissected trifoliate leaves of *Acer*, especially of *A. Negundo* L. and *A. glabrum* Torrey approach this type. The greatest degree of similarity, however, is found with various species of *Rhus*, especially with *R. trilobata* Nutt. and to some extent with *R. Toxicodendron* L. The fossil differs from *R. trilobata* chiefly in having the small basal lobes arising almost or quite at the top of the petiole.

No similar species of *Rhus* have been previously reported from the western Miocene. As pointed out by Brown (2) the leaf described as *R. diluvialis* Arnold from Carter Creek is probably a specimen of *Acer Osmonti* Knowlt.

Aceraceae

Dipteronia insignis (Lesq.) Brown. (Plate 28, fig. 7). A single specimen that unfortunately has a small portion missing appears to be identical with the samaras figured by Brown (1) as *Dipteronia insignis*. He says that this species is related to *D. sinensis* Oliver of central and western China. No leaves referable to this species have been detected in the Sucker Creek material.

Acer Bendirei Lesq. (Plate 29, fig. 4) Under this name Brown (1) includes the leaves and fruits of *Acer* previously designated by several different names, that appear related to *A. macrophyllum* Pursh. Three samaras but no leaves referable to this species, are included in my Sucker Creek collections.

Acer Bolanderi Lesq. (Plate 28, fig. 5; Plate 29, fig. 8). This species is represented by several small specimens that are closely similar to the small leaves figured by Lesquereux (6) from the Auriferous Gravels of California. The leaves are trilobate, with entire or sparsely toothed margins, broadly cuneate base and straight or curved midrib.

The leaves were originally compared with *A. tripartum* Nutt. as to shape and with *A. grandidentata* Nutt. as to size and consistency. In writing about the specimens from Eagle Creek Chaney (4) pointed out certain similarities with *A. saccharum* Marsh. However, a closer resemblance is evident with *A. Buergerianum* Miq. (Plate 28, fig. 4). The leaves studied were taken from plants growing at the Botanical Gardens of University of Michigan. The leaves of this species are like the fossils in the small size, prominent primary veins, character of the lobes, and the weak or obscure tertiaries. *A. Buergerianum* is native to Japan and China.

Acer negundoides MacG. (Plate 29, fig. 5). This species was described from seeds that resemble those of the living *A. Negundo* L. It was described by Mac Ginitie (7) from Trout Creek and has since been reported from a number of western Miocene localities. The samaras do not usually occur in association with perfect leaflets and few figures of the leaves have been given. LaMotte (5) has recently figured a complete leaflet of an *A. Negundo* type found in association with the fruits. His collection contained a single lateral leaflet that differs in several particulars from the one figured here. The leaflet of *A. Negundo* figured (Plate 29, fig. 2) for comparison was taken from a tree at the Botanical Gardens of the University of Michigan and came from Nebraska. No samaras referable to this species have been noted in this collection.

Explanation of Plate 29

Fig. 1. *Quercus malheurensis* H. V. Smith. Type; Mus. Paleont., Univ. of Mich. no. 20010.

Fig. 2. *Acer Negundo* L. Leaflet from Botanical Gardens, Univ. of Mich.

Fig. 3. *Betula Bendirei* Knowlt.

Fig. 4. *Acer Bendirei* Lesq.

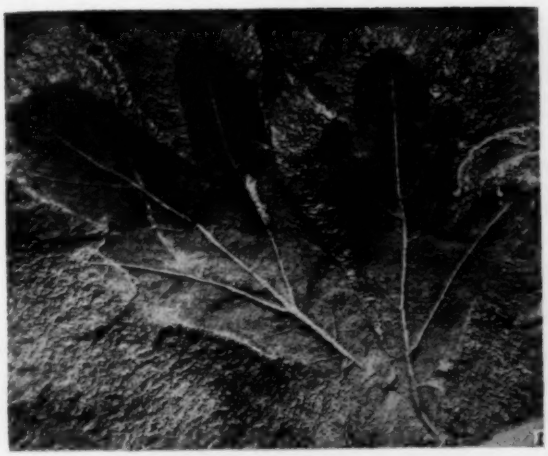
Fig. 5. *Acer negundoides* MacG.

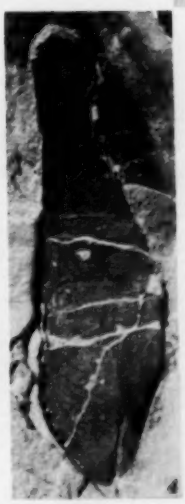
Fig. 6. *Ptelea enervosa* H. V. Smith. Type; Mus. Paleont., Univ. of Mich. no. 20011.

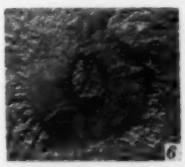
Fig. 7. *Ptelea mollis* M. A. Curtis var. *cryptoneura* Bartlett. Specimen from McDuffie Co., Georgia, in Herbarium, Univ. of Mich.

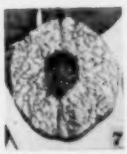
Fig. 8. *Acer Bolanderi* Lesq.

Fig. 9. *Rhus oregonensis* H. V. Smith. Type; Mus. Paleont., Univ. of Mich. no. 20012.









Cornaceae

Nyssa oregonensis n. sp. (Plate 28, fig. 2). Leaves subcoriaceous, 9.5 cm. long, 4.3 cm. broad; ovate, widest about the middle, tapering to an acuminate apex and cuneate base; margin entire; midrib fairly strong, straight or slightly curved, secondaries about 10 pairs, parallel, alternate or occasionally subopposite, arising at an acute angle, finer nervation a very fine distinct reticulum.—Type no. 20015 Mus. Paleont., Univ. of Mich. Collected near Rockville, Oregon.

This sub-coriaceous entire-margined leaf is similar to leaves of *Benzoin aestivale* (L.) Nees and *Diospyrus virginica* L., but is still more like certain leaves of *Nyssa aquatica* L. (Plate 28, fig. 8). This single specimen leaves little doubt as to the presence of *Nyssa* of the *N. aquatica* type in the Sucker Creek beds. No fruits of *Nyssa* are included in this collection.

Three leaf species of *Nyssa* have been described from the western Miocene, but all differ in significant ways from this species. *N. crenata* Chaney from Bridge Creek and Eagle Creek has a crenate margin, a greater regularity in the spacing of the secondaries, and has percurrent tertiaries. *N. hesperia* Berry differs markedly from this species in the less regular venation, the arching of the secondaries well within the margin, the percurrent tertiaries and in the much broader shape. *N. Knowltoni* Berry is more elliptical, has a more prominent midrib and distinctly percurrent tertiaries.

The five modern species of *Nyssa* are native to southwestern Asia and southeastern America. *N. aquatica* occurs in cypress and other swamps from Virginia to Missouri and southward to Florida and Texas.

UNIVERSITY OF MICHIGAN,
ANN ARBOR, MICHIGAN

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New species of cacti from Guatemala, Mexico and Texas*

ELZADA U. CLOVER

(WITH 7 FIGURES)

Echinocereus Gentryi sp. nov. (figs. 1, 2, 3). Caespitosus, caulibus 2–4, decumbentibus vel erectis, 6–15 cm. altis, 2–2.5 cm. crassis; costis 5, rectis, summitate spiralibus, vix tuberculatis; spinis 8–12 lateralibus radiatis, porrectis, acicularibus, albis vel fuscis; centrali saepe solitaria; omnibus fuscis; basi bulbosis, deciduis; areolis 1 mm. latis, rotundis; floribus magnis, 6–8 cm. longis, 5–6 cm. latis, roseis; segmentis perianthii 5-seriatis, stylo albo; stigmatis lobis 8, viridibus; filamentis numerosis, antheris rufis; fructibus viridescentibus. Specimen typicum vivum ex loco "Saucito" dicto in Sonora, Mexico conservatum est in Horto Botanico Universitatis Michiganensis; atgru floribus siccis in Herb. Mich.

Echinocereus Gentryi n. sp. (figs. 1, 2, 3). Caespitose, stems procumbent to ascending, few, jointed 6–15 cm. high, 2–2.5 cm. broad; ribs 5, indistinct, spiral, especially toward the top, tubercles scarcely visible; areoles minute, 1 mm. or less across, circular, 3–4 mm. apart; radial spines 8–12, acicular, 1–2 mm. long, bulbous at the base, more or less deciduous, on very young stems white, often 4–5 mm. long; on new growth of older stems, shorter, brownish; young areoles white wooly, in age naked; central spine usually solitary, rarely 2–5, similar to radials, sometimes darker brown; blossoming in April from areoles 5 to 7 cm. from the tip, flower funnelform, 6–8 cm. long, 5–6 cm. across, tube 3–4 cm. long, perianth segments in 5 whorls, the outer ones bract-like, curling back, olive-drab, inner segments amaranth pink to Tyrian pink, lanceolate, apiculate; style exerted, white to very pale green, stigma lobes 7–8, emerald green; filaments pink above, white below; anthers red; pollen deep yellow; ovary globose, 1.5 cm. across at maturity, greenish, bracts very small, olive-drab, areoles circular, containing somewhat cobwebby wool, spines 8–20, white to pinkish brown, 4–5 mm. long, longer on flower tube than on ovary.

Flowers in the greenhouse open fully about 3:00 p.m. and remain almost fully open all night.

This species is apparently closely related to *E. subinermis* described by Salm-Dyck in 1856 from Chihuahua, Mexico. That species, however, has a shorter flower tube, style included, and is yellow. The author was unable to get either herbarium of living specimens of *E. subinermis*, since it apparently has never been recollected. Comparisons were made from descriptions and photographs. This new species was collected at Saucito, Sonora, Mexico by H. S. Gentry in 1932.

Echinocereus Steereae sp. nov. (fig. 4). Simplex vel caespitosus, caulibus erectis, 8–12 cm. altis, ca. 6 cm. crassis; costis 16–18, tuberculis parvis; spinis

* Papers from the Department of Botany and the Botanical Gardens of the University of Michigan, No. 662.

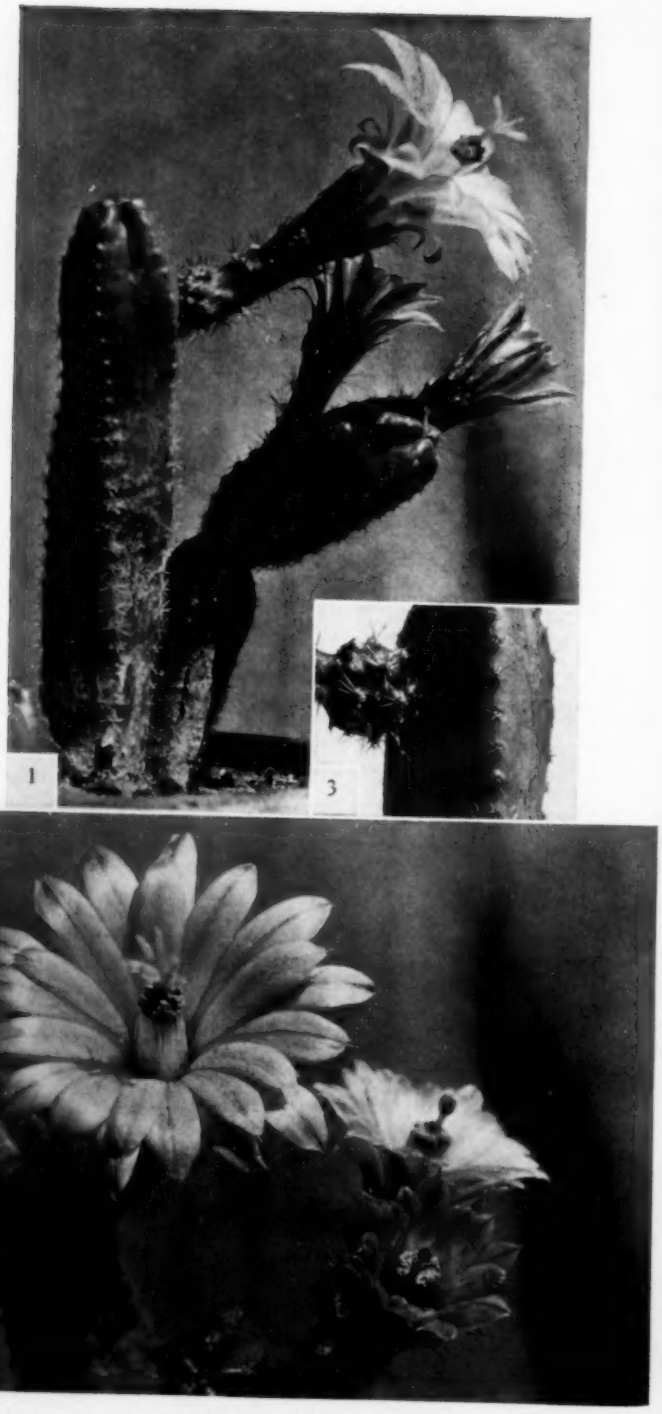

Fig. 1. *Echinocereus Gentryi* in flower. (About two thirds natural size.)
Fig. 2. Flowers of same.
Fig. 3. Fruit of same. (About natural size.)

lateralibus 16–24, acicularibus, albis vel rosaceis, centralibus plerumque 3–5, in serie singula verticali dispositis, areolis ellipticis; floribus magnificis, 10–11 cm. longis, 14–15 cm. latis, segmentis perianthii 5-seriatis, exterioribus, fusco-olivaceis margine, pallide viridibus parte media roseopurpureis; stylo viridi; stigmatis lobis 12; filamentis viridibus; antheris luteis; fructibus ignotis. Specimen typicum vivum ex Montibus Texensibus "Chisos" dictis conservatum est in Horto Botanico Universitatis Michiganensis, Ann Arbor, Michigan; atque floribus siccis in Herb. Mich.

Echinocereus Steereae n. sp. (fig. 4). Plant simple or caespitose, with pinkish white appearance, not at all banded, largest stem seen 12 cm. long, 6 cm. across; ribs 16–18, tubercles distinct, small, flattened dorso-ventrally, alternating with those on adjoining ribs; areoles short-elliptic, if young densely white-wooly (wool lacking in older areoles), 5–7 mm. apart; radial spines 16–24, interlocking, 3–5 spines at the upper end of areole shorter, others about equal, spreading and slanting downward at an angle of 45 degrees; central spines 3–5, usually in a single row, bulbose at the base, shorter than the lower radials, stouter than the upper radials, usually a deeper pink. Flowering in April from areoles almost halfway up the stem to within 3 cm. of the top; flowers ascending or standing at right angles to the stem, very showy, 10–11 cm. long, 14–15 cm. across; perianth segments in 5 whorls, the inner three rose-purple with whitish margins, 7–7.5 cm. long, 2 cm. across near center of segment, very narrow at the base and obtuse to cuspidate at the tip, somewhat erose; tinged with greenish-yellow toward the inside center, grading to deep turtle green at the center; outermost segments uneven, 1.5–3 cm. long, tapering to a very narrow tip, olive-drab in midline, pale green and petal-like at the smooth margin, second whorl 5–7 cm. long, olive-drab in midline, pale green tinged with rose-purple toward the margin; style extending 1 cm. beyond the stamens, white, 2 mm. in diameter, included, stigma lobes dark green, 12, somewhat fused, slightly recurved, decurrent; filaments greenish, anthers pale yellow; ovary 5 cm. long, 1.75 cm. across, its areoles 1 cm. apart, circular, prominently white-wooly, with spines 14–15, spreading, rigid, acicular, 4–5 mm. long, white with brown tips; bracts bright green, tipped with pink, 2 mm. long, narrow; fruit unknown.

Collected by Mrs. Lois Steere in the Chisos Mts., western Texas, March, 1937.

Rhipsalis Bartlettii sp. nov. (figs. 6, 7). Ramosissima, ramis pendulis, filiformibus, dichotomis, rarius verticillatis, pallide viridibus; areolis prominentis, dense lanatis, lana lutea-fusca; fructibus albis, globosis. Specimen typicum siccatum legit H. H. Bartlett sub numero 12720 ex "Uaxactun," Petén, Guatemala, in Herb. Univ. Mich.

Rhipsalis Bartlettii n. sp. (figs. 6, 7). Hanging epiphyte, branches 2 m. long, weak and pendent, branching dichotomous, sometimes verticillate, light green, outer joints often less than 1 mm. in diameter, areoles prominent, filled with

Fig. 4. *Echinocereus Steereae* in flower. (Slightly less than natural size.)

Fig. 5. *Deamia diabolica*.

Fig. 4. *Echinocereus Steereae* in flower. (Slightly less than natural size.)

Fig. 5. *Deamia diabolica*.

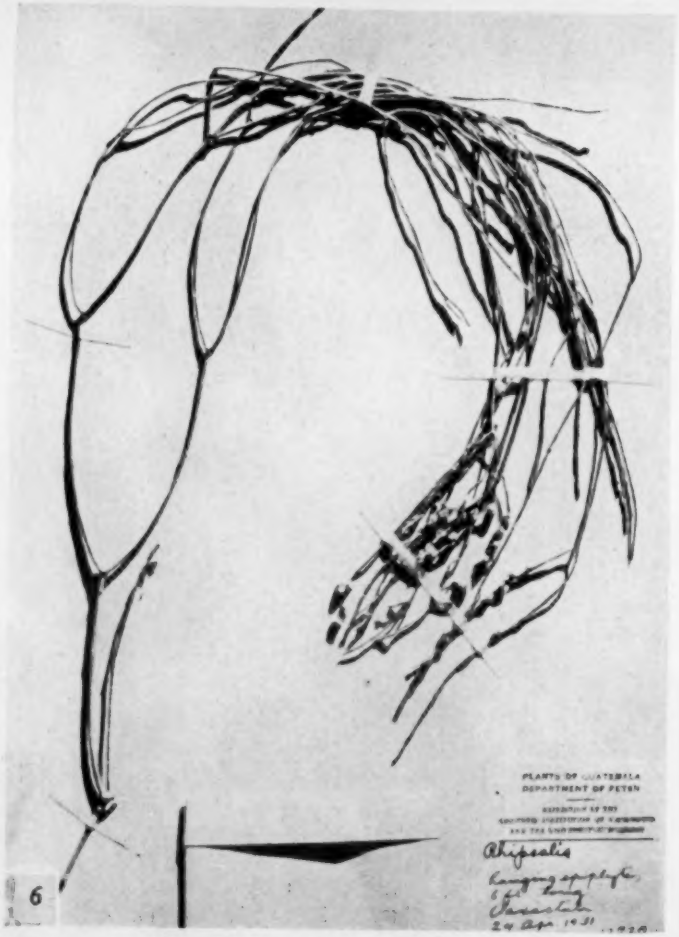

Fig. 6. Habit of *Rhipsalis Bartlettii*.

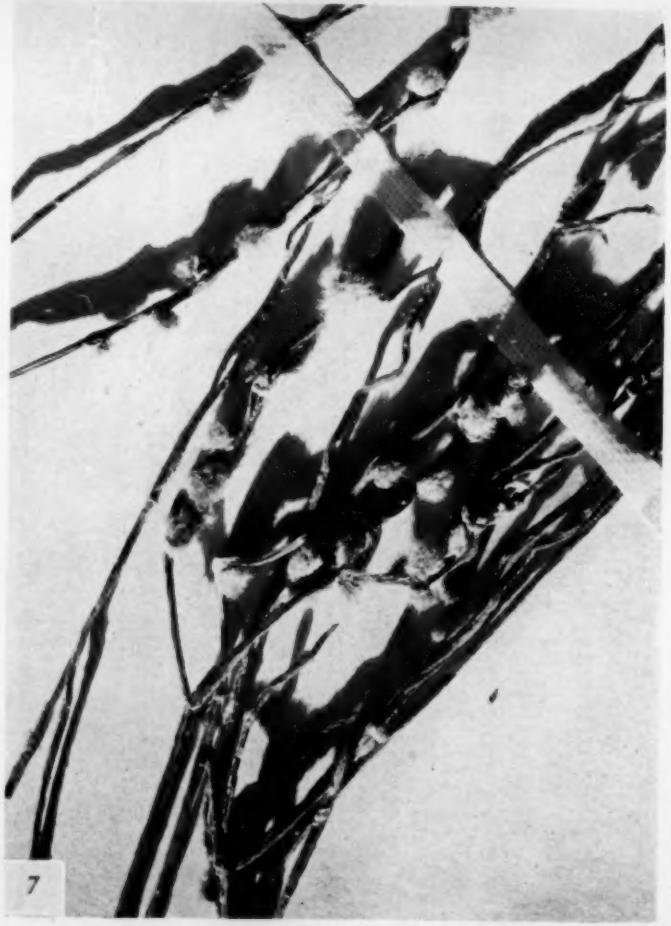

Fig. 7. Detail of same showing prominent areoles.

dense masses of tawny hairs, these 2–3 mm. long; flowering areoles not lanate, ovary sunken in the branch, fruit white, globose, 3–4 mm. in diameter; seeds black, reniform, less than 1 mm. long, testa reticulate furrowed. Flower unknown. Specimens were collected by H. H. Bartlett, Uaxactun, Petén, Guatemala, April 24, 1931. A single less ample specimen was collected for the University of Michigan Herbarium by E. Matuda at Cordoba, Vera Cruz, Mexico, August 14, 1936.

Deamia diabolica sp. nov. (fig. 5). Planta fruticulosa volubilis probabiliter ut in *D. Testudine* densissime epiphytica in arboribus humilibus prope litora, inferne ramosissimis, ramis radicantibus; costis 4–5 altissimis alatis, acutis, subcrenatis; spinis 12–20, dissimilibus, 5–52 mm. longis, acicularibus vel nonnihil triquetris, basi bulbosis, fuscis; floribus albis, 22–24 cm. longis tubo 9–11 cm. longo, setoso; ovario spinoso. Specimen typicum siccatum in Herb. Mich., Ann Arbor, Mich.

Deamia diabolica n. sp. (fig. 5). Stems robust, jointed, 3–4 angled, ribs thin and wing-like 3–4 cm. high, subcrenate, areoles on edges of wings 1.5–2 cm. across on mature stems; spines stout, various, 5–52 mm. long, brown, becoming grayish, bulbose at the base, acicular, terete to somewhat 3 angled, longer ones slightly curving, one spine in an areole often much longer than others; flower 22–24 cm. long, white, tube about 12 cm. long, bracts on tube small, areoles 1.5 cm. apart above, closer below, filled with tawny wool and usually 3 brown to yellowish, curling hairs 1–3 cm. long; inner perianth segments white, spathulate, apiculate, outer segments much shorter, linear greenish-white; style stout, extending beyond the stamens, stigma lobes 7; ovary ovate, densely spiny, spines golden-brown, acicular, interlocking, 3–5 cm. long, semi-rigid, areoles circular, filled with tawny wool; seeds about 2 mm. long, brown, shiny, subreniform, testa slightly reticulate. Specimens collected by Percy Gentle in the Corozal District, British Honduras, 1931–32. No. 490. Additional specimens were collected by Mercedes Aguilar La Libertad, Petén, Guatemala, June 7, 1934, no. 262.

Notes on American melastomes, including nine new species

H. A. Gleason

Rhynchanthera paludicola comb. nov. *Tibouchina paludicola* Donn. Sm. Bot. Gaz. **42**: 293. 1906. In his original description the author mentioned the five sterile stamens and the slender beaks of the fertile anthers and remarked that these were abnormal characters for the genus. They are however perfectly normal characters for *Rhynchanthera*, section *Isostemones*. The species is related to *R. Hookeri* of the northern Andes, from which it differs in its larger flowers, much longer sepals, and the fewer and much longer glandular hairs of the hypanthium.

The only other North American species of the genus *Rhynchanthera* is *R. mexicana* DC., of southern Mexico and Panama. This is a member of the section *Anisostemones*, in which the connective of one stamen is greatly prolonged.

The genus *Centradenia* was credited with four species by Cogniaux in 1891. This number may now be increased to seven, all natives of the mountains and adjacent foothills of Mexico and Central America, extending south as far as Panama. The generic description given by Cogniaux needs a slight revision: the anthers are sometimes quite isomorphic; while often oblong or ovoid, as stated, they may also be linear-oblong or subulate, and in these narrower forms are acuminate.

Brandegee's two species, *C. chiapensis* and *C. salicifolia*, are both valid and belong to the section *Eucentradenia*, characterized by strongly dimorphic anthers. *C. chiapensis* and *C. grandifolia*, with ebracteate flowers, glabrous hypanthium, and wide, strongly falcate leaves, are clearly related. In the latter the leaves are 4-nerved and the stem prominently winged; in the former the leaves are 3-nerved or 5-nerved and the stem merely 4-angled. *C. salicifolia* and *C. Bernoullii*, with glandular hypanthium and fairly broad leaves, are also related. In the latter the appendages of the larger stamens are terminated by two slender elongate lobes or setae, while in the former they are merely shallowly lobed.

In the section *Centradeniopsis*, characterized by stamens isomorphic or nearly so, a seventh species may now be described, differing from *C. floribunda* in its linear-subulate anthers with truncate appendages:

Centradenia Maxoniana sp. nov. Caules graciles, erecti (?), subflexuosi, subteretes, dense strigosi, pilis subulatis 0.6 mm. longis e basibus satis tumidis. Petioli foliorum majorum graciles, 2–5 mm. longi, strigosi. Laminae firmulae, supra virides, subtus pallidiores, lanceolatae, usque 10 cm. longae 2.2 cm. latae, acuminatae, integrae, paulo falcatae, basi inaequilaterales, latere uno longe cuneatae, altero obtusae vel rotundatae, 4-pli-nerviae, venis supra fere

planis subtus paulo elevatis, supra setosae, pilis gracilibus circa 0.5 mm. longis, subtus superficie glabrae ad venas strigosae, pilis rigidis 0.8 mm. longis. Folia minora subulata vel anguste lanceolata, 1–2 cm. longa, mox decidua. Cymulae 3–10-florae, caulem et ramulos ex axillis superioribus terminantes, pedunculis pedicellisque dense glanduloso-pubescentibus, pedicellis 3–5 mm. longis. Hypanthium anguste campanulatum, 8-costatum, 3.5 mm. longum, glanduloso-pubescens, pilis gracilibus adscendentibus 0.4–0.5 mm. longis, summo setis validioribus ornatum. Sepala triangularia e sinibus late rotundatis, 1 mm. longa, acuta, glabra vel fere glabra. Petala oblonga, 5 mm. longa, inaequilateralia, minute glanduloso-ciliata. Stamina isomorpha sed magnitudine inaequalia; filamenta 2–2.3 mm. longa; thecae lineari-subulatae, fere rectae, 2.8 vel 4 mm. longae, convolutae; connectivum brevissime productum, ad filamenti apicem oblique dilatatum, parte anteriore adscendente, quadrata, 0.5 mm. longa, parta posteriore descendente, ovata, 0.2 mm. longa. Ovarium obovoideo-oblongum, 2.8 mm. longum, glabrum; stylus gracilis, 6 mm. longus.

Type, *Pittier 5414*, collected between Hato del Jobo and Cerro Vaca, eastern Chiriquí, Panama, alt. 700–1000 meters, and deposited in the United States National Herbarium. Other specimens are *Williams 321*, from Panama; *Pittier 11061* and *Tonduz 7628*, from Costa Rica.

The genus *Chaetolepis* is primarily South American, with one species, *C. alpina* Naud., ranging north into Costa Rica. In western Cuba and the Isle of Pines the genus appears again, and from this rather restricted area Cogniaux recognized four species, *C. saturaeoides* Triana, *C. cubensis* Triana, *C. brevistrigillosa* Cogn., and *C. Grisebachii* Cogn. Careful examination of the ample material preserved in American herbaria has failed to disclose any reliable evidence which might indicate specific differences among them. They have been separated on such notoriously variable characters as the proportions and density of pubescence on the leaves, the shape and number of scales and hairs on the stem and hypanthium, the size and shape of the sepals, and the number of flowers, and in all of these features they intergrade freely. I therefore propose their union into a single species under the oldest specific name, *Chaetolepis cubensis* (A. Rich.) Triana.

The generic name *Heeria* was maintained by Triana and by Cogniaux because of its supposed priority of one year over *Heterocentron*, and in spite of the fact that *Heeria* was a later homonym. The next available name is apparently *Heterocentron*, which was used by Krasser and by Rose. Actually *Heterocentron* was published in 1838, a year earlier then *Heeria*, so that there can be no doubt of the proper name for this genus of Mexican and Central American plants.

Of greater importance is the possible segregation of the genus into two,

as was recommended by Rose, who very properly adopted *Schizocentron* Meissn. for the smaller group. In it the plants are decumbent or creeping, instead of erect, the flowers are solitary, instead of paniculate, and in the better known species the leaves are 3-nerved, instead of multipli-nerved. These characters give the plants an entirely different facies, but they are not supported by floral structures. In consistency with the standards used elsewhere in the family, the two groups must be kept within a single genus, as was done by both Triana and Cogniaux.

Cogniaux admitted six species in 1891. Since then four species have been added, *H. occidentalis* Rose in 1905, *H. suffruticosa* Brandg. in 1914, *H. alata* Rose & Standl. and *H. laxiflora* Standl. in 1924. I shall here describe four species as new, make two segregations from species previously recognized but recently united, and combine two old species into one, leaving the genus with fifteen species as recognized by me.

Heterocentron subtriplinervia, originally described by Link & Otto in the genus *Melastoma*, is the most abundantly represented species in most herbaria. In transferring the species to *Heterocentron*, Braun and Bouché noted that the difference between it and *H. rosea* was slight, the latter having an ovarial crown of four scales which was lackng in the former. Examination of an excellent series of specimens shows that this character is variable and that no other constant character can be found to separate them. *H. rosea* is accordingly reduced to synonymy.

The section *Euheeria* contained a single species, *H. elegans* (Schlecht.) Kuntze, in 1891. To this Brandegee added in 1914 an excellent species, *H. suffruticosa*, its hypanthium strigose with non-glandular hairs, rather than glandular-hirsute, and its leaves multipli-nerved, rather than 3-nerved. A third species of the group may now be described, agreeing with *H. elegans* in the characters above mentioned but differing in its sessile upper leaves and in its sepals exceeding the hypanthium.

Heterocentron sessilis sp. nov. Fruticulus, caulibus gracilibus elongatis sarmentosis, subteretibus sed angustissime 4-alatis, sparse strigosis praesertim ad alas; internodia usque 5–10 cm. longa. Petioli graciles, 2–4 mm. longi, sparse strigosi. Laminae ovatae vel ovato-oblongae, 15–25 mm. longae 8–12 mm. latae, acutae, crenatae, ad basin late acutae usque rotundatae, 3-nerviae, supra et ad venas venulasque subtus sparse setosae, venis secundariis more Melastomatacearum nullis sed vena media venulas laterales curvatas emittenti; foliorum juga 1 vel 2 superiora sessilia, lata ovata, circa 8 mm. longa 5 mm. lata, basi rotundata vel subcordata. Flores solitarii, ramos laterales terminantes, pedunculis 2–3 cm. longis glabris gracilibus. Hypanthium campanulatum 4 mm. longum hirsutum, pilis patulis vel subreflexis 1.5 mm. longis basi incrassatis. Sepala erecta vel adscendentia, triangulari-lanceolata,

acuminata, minute ciliata, ceterum glabra, hypanthium paulo excedentia. Petala rubro-purpurea 10 mm. longa. Stamina modo generis. Ovarium apice glanduloso-setosum.

Type, *von Türckheim II 1554*, collected at Coban, Dept. Alta Verapaz, Guatemala, alt. 1550 meters, and deposited in the Gray Herbarium of Harvard University. *Von Türckheim 2470* in the Field Museum and the National Herbarium is the same. The type number in the Field Museum and the National Herbarium, *von Türckheim II 2364* in the same herbaria, and *von Türckheim 2471* in the National Herbarium represent an intermediate form between, and possibly a hybrid of, this species and *H. glandulosum* Schenck. They are characterized by paniculate flowers on short glandular pedicels and by larger leaves, many of which exhibit the multiple venation so characteristic of most species of the genus.

The remaining twelve species of *Heterocentron* may be divided into two groups, one of six species with glandular-hirsute hypanthium and one of five species with strigose non-glandular hypanthium, with a twelfth species of doubtful relationship.

In the first group two species are found in the western part of Mexico, in the states of Jalisco, Durango, Sinaloa, and Nayarit; in these the ovary is not setose at the summit. One of these, *H. mexicana* Hook. & Arn., the type of the genus, was combined by Cogniaux with *H. subtriplinervia*. Examination of original material shows that it is quite distinct. Related to it is an undescribed species, distinguished by glabrous and entire sepals, those of *H. mexicana* being glandular-ciliate and usually also pubescent on the back. It also differs in its larger panicle, its much larger flowers, and the stouter hairs of the hypanthium. This is:

Heterocentron floribunda sp. nov. Caules erecti graciles, acute 4-angulati, 4-sulcati, tenuiter canescentes punctis minutis albis, internodiis glabris, nodis sparse setosis. Petioli graciles 5–10 mm. longi, sparse strigosi. Laminae tenues, ovato-ellipticae, pallide virides, 3–6 cm. longae 1.5–3 cm. latae, integrae, utrinque acutae, multipli-nerviae, jugis lateralibus 4 vel 5, supra et subtus ad venas sparsissime setosae, pilis gracilibus circa 0.5 mm. longis. Panicula elongata ramosa multiflora, ramis angularibus, sparse pubescens, pilis patulis circa 0.3 mm. longis, iis pedicellorum glandulosis; pedicelli supremi fere glabri, 5–8 mm. longi, bracteis 2 subulatis 1.5–2 mm. longis sustenti. Hypanthium late campanulatum, 4.3 mm. longum, pubescens, pilis patulis vel curvato-adscendentibus glandulosis 0.4–0.6 mm. longis, e basibus depresso-conicis 0.3–0.4 mm. altis. Sepala ovato-lanceolata vel triangularia, 5.5 mm. longa, basi 2.5 mm. lata, anguste acuminata, glabra, integra. Petala late obovata, 9 mm. longa 8 mm. lata, integra, venosa, conspicuiter inequilatera, vena media curvata. Filamenta gracilia, 4.5 vel 6 mm. longa; thecae 3.5 vel 4.6 mm. longae; connectiva staminum exteriorum paulo curvata, 2.7 mm. longa, infra

thecas paulo incrassata, appendice complanata, anguste clavata, obtusa, 2.4 mm. longa. Ovarium liberum glabrum; stylus sigmoideus 7 mm. longus.

Type, *Ortega 5329*, collected at Sianori, Durango, and deposited in the United States National Herbarium. Other collections, all from Durango, are *Ortega 4272*, *Palmer 102*, and *Rose 3509*.

The remaining four species in the group are natives of more southern regions, ranging from Jalisco to Costa Rica. Two of them, *H. glandulosa* Schenck and *H. axillaris* Naud., have glabrous entire sepals. They were united by Cogniaux, but may be distinguished specifically by the glandular-hirsute pedicels of the former and the strigose non-glandular pedicels of the latter.

The last two have glandular-pubescent, glandular-ciliate sepals. In *H. undulata* Naud. the setae of the ovary are non-glandular, the sepals are shorter than the hypanthium, and the connective of the longer stamens is half as long as its appendage. In the other, described below as new, the ovarian setae are glandular, the sepals exceed the hypanthium, and the connective is longer than the appendage.

Heterocentron salvadorana sp. nov. Suffruticosa, 1 m. alta, caulibus acute 4-angulatis, supra tomentulosis, demum glabrescentibus. Petioli 5–8 mm. longi. Laminae firmulae, ovato-ellipticae, 3–7 cm. longae 2–3 cm. latae, obtusae, integrae, basi late cuneatae, multipli-nerviae, utrinque tenuiter pubescentes. Panicula magna multiflora, pedicellis brevibus dense glandulosis. Hypanthium subglobosum, 2.8 mm. longum, dense glanduloso pubescens, pilis patulis 0.3 mm. longis. Sepala ad anthesin reflexa, ovata, 3.2 mm. longa, basi 2.2 mm. lata, apice involuta, glanduloso-ciliata, ciliis 0.1 mm. longis, glanduloso-pubescentia. Petala late obovata, 5 mm. longa 4 mm. lata, glanduloso-ciliata, pilis 0.1 mm. longis. Filamenta 4 vel 5.5 mm. longa; thecae 2.8 vel 3.5 mm. longae; connectivum staminum majorum supra filamentum fere rectum 2 mm. longum, infra filamentum in calcara 2 subulata divisum. Ovarii squamae semicirculares erectae, 0.4 mm. altae, densissime glanduloso-ciliatae, pilis fere contiguis, usque 0.8 mm. longis, fructu persistentibus.

Type, *Standley 20398*, collected at Santa Ana, Dept. Santa Ana, Salvador, and deposited in the United States National Herbarium.

Recent collections from Chiapas have disclosed a fourth undescribed species, marked by excellent morphological characters but of doubtful relationships. This is:

Heterocentron muricata sp. nov. Caulis partes superiores acute 4-angulatae, glabrae vel levissime strigosulae, ad nodos dense breviterque barbatae. Laminae membranaceae, oblongae, 2–4 cm. longae, 1–2 cm. latae, breviter abrupteque acuminatae, ad basin late cuneatae in petiolum brevem superne alatum, supra minutissime strigosulae, subtus sparse strigosae, praecipue ad

venas. Ramuli floriferi ex axillis superioribus divaricati, pauciflori, superne strigosi; pedicelli veri 4–8 mm. longi gracillimi glabri. Hypanthium subglobosum, 4.5 mm. longum, valde muricatum, muricis ca. 1 mm. longis, ceterum glabrum. Sepala anguste triangularia 6.5 mm. longa, ad anthesin reflexa, nunc integra, nunc brevissime sparseque ciliata. Petala staminaque non visa, sed connectivum unum 1.9 mm. longum alte bilobum, anthera unica 2.6 mm. longa. Ovarium apice squamis 4 quadrato-ovatis glanduloso-ciliatis coronatum; stylus gracilis sigmoideus 8 mm. longus, stigmate punctiformi.

Type, *Matuda 1967*, collected at Montecristo, Chiapas, January, 1938, without further data, and deposited in the Britton Herbarium at the New York Botanical Garden. Although in general habit our plant somewhat resembles *H. suffruticosa* Brandg., also from Chiapas, it differs notably in its muricate hypanthium and its squamiferous ovary. The latter feature indicates a possible relation to the group of five species mentioned previously, including the common *H. subtriplinervium* A. Br. & Bouché, but none of this group has a muricate hypanthium. Stoutly subulate hypanthial hairs are characteristic of *H. undulata* Naud., but in that species glandular pubescence is abundant, the hypanthium is much smaller, and the sepals only 2–2.5 mm. long.

David Don established the genus *Arthrostemma* in 1823, crediting it to Pavon, and including five species which are now assigned to three different genera in as many different tribes of the family. As a result, it accumulated many unrelated species during the next fifty years, and several of its species were segregated under various generic names. Triana accepted the genus in the sense of Ruiz and Pavon in 1871 and it was so continued by Cogniaux in 1891. Three North American species were recognized by Cogniaux, *A. fragile* Lindl., *A. campanulare* Triana, and *A. parvifolium* Cogn.

The characters of the genus, as regularly understood since the work of Triana, are definite. The flowers are 4-merous, with slender elongate hypanthium and short triangular sepals; petals large, fugacious or caducous; stamens dimorphic; anthers linear; connective conspicuously prolonged below the thecae, bearing a large anterior appendage, 2–3-toothed or lobed at its apex; ovary free, 4-celled.

Triana described *A. alatum* in 1871 from Venezuelan material without flowers. Flowering specimens are now available from Panama and Salvador and show that the anthers are nearly isomorphic, quite small, ovoid in shape, with a very short connective bearing a subulate spur. Notwithstanding these discrepancies, the plant is obviously a good *Arthrostemma*, and the generic description must be revised accordingly.

Cogniaux described *A. parvifolium* from Guatemalan material without flowers, and in 1904 Donnell Smith described *A. apodocarpum* from the

same country. Comparison of the types shows that these two species are identical. Smith dismissed the structure of the anthers in five words, "stamina parva inaequalia" and "antheris parvulis." Here also they are short, ovoid in shape, nearly isomorphic, with a short connective bearing a flat truncate spur. Clearly *A. alatum* and *A. parvifolium* are closely related. In the latter the leaves are acute to cuneate at the base and the filaments are glandular-pubescent; in the former the leaves are rounded to subcordate at the base and the filaments are glabrous.

A. hirtellum Cogn. was described from Guatemalan material in fruit. So far as known to me, it has been collected but once and I have seen three specimens of this type collection. Flowers are absent, although Cogniaux describes the anthers in terms that might well apply to an *Arthrostemma*, but without stating dimensions or proportions. The plant differs notably from all other species of the genus in its short, broadly campanulate hypanthium, its elongate sepals, and its setose ovary, and there can be little doubt that it is not an *Arthrostemma*. Its generic affiliation cannot be settled until flowering material can be examined.

The well known name *Arthrostemma campanulare* Triana (1871) is not tenable, being a later homonym antedated by *Arthrostemma campanulare* DC. (1828). It has been replaced by *A. macrodesmum* Gl.; Williams, Fl. Trin. & Tob. 356, 357. 1934.

The genus *Monochaetum* is represented in North America by seventeen species, all montane or subalpine in their distribution. Two of these are known only from recent collections and are described below. They suggest that further exploration in the less accessible mountains of Central America may reveal still other species.

Monochaetum compressum sp. nov. Frutex ramosissimus usque 2 m. altus, caulibus gracilibus hirsutulis, pilis e basibus papillosis leviter retrorsis, internodiis 5–10 mm. longis. Petioli 1–3 mm. longi patentim hirsuti. Laminae firmulae oblongae vel oblongo-lanceolatae, 5–17 mm. longae 3–6 mm. latae, acutae vel obtusae, integrae, basi obtusae vel rotundatae, levissime 3-plinerviae, supra virides sparse strigosae, venis primariis leviter impressis, secundariis obsoletis, subtus pallidae molliter villosae, venis secundariis obscuris reticulatis. Flores solitarii, ramulos breves terminantes, pedicellis hirsutis, quam hypanthio brevioribus. Hypanthium fusiformi-campanulatum 8–9 mm. longum, sparse hirsutum, pilis eglandulosis patulis 0.6–0.8 mm. longis e basibus papillosis. Sepala patentia oblongo-triangularia, 5.6 mm. longa 2.4 mm. lata, ciliata, dorso sparse hirsuta, pilis non papillatis. Petala pallide purpurea circa 15 mm. longa. Stamina interiora: Filamenta 10 mm. longa; antherae erectae subulatae 6.2 mm. longae; appendices adscendentes oblongae 3.3 mm. longae. Stamina exteriora: Filamenta 9 mm. longa; antherae arcuatae 9–10 mm. longae; appendices 5 mm. longae dorso alte canaliculatae, lateribus

adpressis. Ovarium summo villosum, pilis erectis 0.9 mm. longis; stylus 7.5 mm. longus.

Type, *Skutch 1516*, collected on the south slope of Volcano Atitlan, Dept. Suchitepequez, Guatemala, alt. 2400 meters, and deposited in the Britton Herbarium at the New York Botanical Garden. In its freely branched stem and small leaves, *M. compressum* has a superficial resemblance to *M. Deppeanum* Naud. It differs from that species in its larger anthers and in the shape of its anther-appendages. These features, together with its large flowers and papillate pubescence of minutely barbellate hairs, indicate its relationship to *M. macrantherum* C l. It is distinguished from this species by its hirsute pubescence on stem and hypanthium and by its 3-pli-nerved leaves which are uniformly pubescent on both sides.

Monochaetum rubescens sp. nov. Frutex parce ramosus, caulibus praeter nodos minutissime setosos glabris rubescentibus. Petioli graciles 5–10 mm. longi glabri. Folia membranacea ovato-lanceolata vel ovata, maxima usque 42 mm. longa 19 mm. lata, superiora minora, acuminata, minutissime serrulata, dentibus seta adpressa brevi terminatis, basi acuta vel abrupte cuneata, 3–5-pli-nervia, supra opaca vel rubescentia, glabra, venis primariis angustissime impressis secundariis obsoletis, subtus pallida sparsissime setosa, venis primariis leviter elevatis, secundariis obscuris flexuosis. Flores 1 vel 3, caulem et ramos 2 supremos terminantes, pedicellis quam hypanthio dimidio brevioribus glabris. Hypanthium campanulatum rubro-purpureum 7 mm. longum, glabrum praeter setas paucas breves terminales. Sepala patentia rubro-purpurea oblongo-ligulata 7.5 mm. longa 3 mm. lata, acuta, ciliata, setis 1–3 ornata ceterum glabra. Petala purpurea late obovata 20–25 mm. longa. Stamina interiora: Filamenta complanata 10 mm. longa; antherae erectae subulatae 4.4–4.7 mm. longae; appendices curvato-erectae anguste ellipticae 4 mm. longae 0.9 mm. latae. Stamina exteriora: Filamenta 8.5 mm. longa; antherae arcuatae circa 10 mm. longae; appendices ad apicem dilatatae teretes 5 mm. longae. Ovarium ad apicem sparse setosum; stylus glaber 7.5 mm. longus.

Type, *Matuda 0932*, collected at Siltepec, Chiapas, and deposited in the herbarium of the University of Michigan. *Matuda 1015*, from Mt. Pasitar, Chiapas, agrees with the type in every detail. *Matuda 0973*, from Mt. Orando, Chiapas, has somewhat longer leaves, reaching 60 mm. in length and only 20 mm. in width. The few-flowered inflorescence, the almost complete absence of pubescence, and especially the terete appendages of the larger anthers indicate that *M. rubescens* belongs to the species-group

[1] Am. Jour. Bot. **16**: 586–594. 1929.

Pringleae.[1] The three (or possibly four) species hitherto known have shorter sepals and conspicuously strigose or glandular hypanthia.

The huge genus *Miconia*, already with nine hundred described species, continues to receive additions in many parts of its range. The two described below are both well marked and abundantly distinct from the species hitherto known.

Miconia filamentosa sp. nov. Sect. *Eumiconia:* arbuscula; rami superiores teretes graciles, tenuissime stellato-puberuli, internodiis 3–8 cm. longis. Folia in quoque jugo subaequalia. Petioli 2–5 mm. longi, minute stellato-puberuli. Laminae tenues oblongae vel oblongo-lanceolatae vel anguste lanceolatae, usque 12 cm. longae 3 cm. latae, anguste acuminatae, conspicue obcrenatae, ad basin minute cordulatam angustatae, 3-nerviae vel fere 3-pli-nerviae, supra glabrae, subtus ad venas sparsissime stellato-puberulae, venis secundariis 2–3 mm. dissitis sub angulo 80° divergentibus. Panicula terminalis, 6–8 cm. longa lataque, ubique densiuscule stellato-puberula, ramis oppositis divaricatis, ad nodos omnes lineari-bracteolata, bracteolis 0.8 mm. longis. Flores 5-meri, sessiles in cymulis trifloris sed flores laterales ut videtur pedicellati. Hypanthium obconicum, ad torum 1.8 mm. longum, stellato-puberulum. Calycis tubus nullus vel usque 0.2 mm. longus, sepalis e sinibus acutis semicircularibus vel triangularibus, 0.5 mm. longis, rotundatis vel acutis, minutissime ciliatis, dentibus exterioribus crasse conicis. Petala anguste obovato-oblonga, 3 mm. longa 1.3 mm. lata, glabra, paulo retusa. Stamina dimorpha. Filamenta gracillima, 4.6 vel 2.3 mm. longa. Antherae lineares, 3 vel 2.3 mm. longae, poro terminali latiusculo dehiscentes. Connectivum staminum majorum infra thecas 0.7 mm. productum et in lobum obliquum rotundatum, filamentum fere amplectentem expansum, staminum minorum 0.4 mm. productum et in lobum 1 rectum dorsalem et lobos 2 laterales deflexos divisum. Ovarium semiinferum, 4-loculare, summo rotundatum, minute pubescens, obscure 10-lobatum, ovulis in quoque loculo circa 8; stylus gracilis glaber, 5.5 mm. longus; stigma minute capitatum.

Type, *Klug 938*, collected at Mishayacu, near Iquitos, Dept. Loreto, Peru, in forest at an altitude of 100 meters, and deposited in the Britton Herbarium at the New York Botanical Garden. In *Williams 3306*, a fruiting specimen with less crenate leaves and a panicle up to 20 cm. long, the fruit is spherical and about 2 mm. in diameter. In *Krukoff 8936*, from São Paulo de Olivenca, Brazil, the flowers and pubescence are essentially identical with the type, but the leaves are much broader at the base and deeply cordate, consequently appearing subsessile. *M. filamentosa* has been compared with practically every described species of the section. It is probably nearest to *M. Sprucei* Triana, in which the leaves are much wider, more abruptly acuminate, essentially entire, and entirely lacking the heart-shaped base.

Miconia incurva sp. nov. Sect. *Amblyarrhena:* frutex 9 m. altus, caulibus, petiolis, foliorum pagina inferiore, inflorescentia, hypanthiis, et calycibus ferrugineo-stellato-tomentosis. Rami graciles demum glabrescentes, internodiis 1–2 cm. longis. Petioli satis graciles 5–10 mm. longi. Laminae tenues, oblongo-lanceolatae, maximae 13 cm. longae 3.5 cm. latae, anguste acuminatae, integrae, basi obtusae vel late acutae, 3-pli-nerviae ca. 1 cm. supra basin, supra glabrae; venae primariae supra impressae, submarginalibus validis, secundariae 2–3 mm. dissitae, sub angulo fere recto divergentes. Paniculae ca. 5 cm. longae lataeque, ramis oppositis; bracteae persistentes triangulari-subulatae 2–4 mm. longae; cymulae triflorae. Flores 5-meri. Hypanthium obconicum carnosum, ad torum 6.7 mm. longum, intus obscure costatum. Calycis tubus fere erectus, 3.3 mm. altus, lobis brevissimis truncatis subscariosis, margine libero fere nullo, dentibus exterioribus flexuosis incurvis subulatis 7 mm. longis. Petala alba, late obovata, valde obliqua, basi subunguiculata, 10–11 mm. longa lataque. Stamina isomorpha; filamenta glabra 5.5 mm. longa, medio leviter dilatata, infra antheram subito contracta; antherae oblongae, 4.7 mm. longae, 2-loculares, poro minuto ventrali-terminali dehiscentes, connectivo incrassato non producto. Ovarium inferum 5-loculare, summo concavo circum stylum annulato; stylus crassus teres 14 mm. longus, stigmate capitato subgloboso, 2 mm. diametro.

Type, *Skutch 3273*, collected at Vara Blanca de Sarapiqui, north slope of Central Cordillera, Costa Rica, alt. 1500–1700 meters, and deposited in the Britton Herbarium at the New York Botanical Garden. While the plant is obviously a *Miconia*, with anthers externally resembling the typical form of the section *Amblyarrhena*, it is exceptional for the section in having only two loculi in the anthers. Very few species of the section have elongate exterior teeth, and they differ notably in other structural features.

NEW YORK BOTANICAL GARDEN.

INDEX TO AMERICAN BOTANICAL LITERATURE
1935–1937

The aim of this Index is to include all current botanical literature written by American, published in America, or based upon American material; the word America being used in the broadest sense.

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DR. HAROLD N. MOLDENKE
New York Botanical Garden
Bronx Park (Fordham Branch P.O.)
New York City